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MISCELLANEOUS NOTES ON NEOTROPICAL FLORA XX. A NEW SPECIES
OF *HUMIRIASTRUM*

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ABSTRACT

A new species, *Humiriastrum liesneri* from the Venezuelan Guayana is described.

KEY WORDS: Humiriaceae, *Humiriastrum*, Venezuela

In the continued process of working on the Humiriaceae for the Flora of the Venezuelan Guayana, in preparation by the Missouri Botanical Garden, a new species of *Humiriastrum* has been found which is here described.

Humiriastrum liesneri Cuatrecasas, *sp. nov.* TYPUS: VENEZUELA. Terr. Fed. Amazonas, Dt. Río Negro, Cerro Aracamuni summit, Proa Camp, medium height, semiopen forest, 1400 m, near rock outcrop in savanna, buds green, 2 m shrub, 28 Oct 1987, *R. Liesner & G. Carnevali 22589* (HOLOTYPE: US; Isotype: MO).

Frutex vel arbuscula circa 2 m alta, dense ramulosa. Rami ultimi densiuscule hirtuli, ascendentes conferte foliosi, denique glabrati teretes brunnescenti-viriduli. Folia crassiuscule coriacea rotundata usque leviter retusa, vel paulo attenuata obtusaque fere subobtrulata, basim anguste acuteque cuneata; margine brevi-crenata leviter incrassata revolutaque; adaxialiter nitida, saltem in juvenili sparse minuteque hirtula, costa signata depressa, nervis secundariis 6 utroque latere aliquando conspicuis vel obsoletis, venulis reticulatis depressis superficie rugosa efferens; abaxialiter primum ferrugineo-viridula minute pilosula, deinde sordide viridis, plerumque glabrescens sed parvis pilis ad basim, reticulo venulorum conspicuo, superficie omnia dense minute glanduloso-granulata; vulgo 3.8-4.8 x 2.7-3.3 cm, sed aliquae minores (2.2-3.0 x 1.5-2.8 cm)

interpositae. Pseudopetiolus 1-3 mm, ad basim dorso incrassato pulvinato-glanduloso.

Inflorescentiae terminales plerumque folia non excedentes, conferte corymboso-paniculatae, 2-4 x 3-4 cm, pedunculo circa 1 cm longo; rami monochasiales aliquando 2-4 inaequales pseudoverticillati; ramusculi terminales breves 1-4 flores ferentes. Flores in speciminibus non evolutis, in gemmatio statu, breviter pedicellati. Pedicelli 0.2-1.0 mm. Rami ramusculi pedicelique densiuscule minuteque hirtuli. Bracteae mox deciduae.

Alabastra viridia subglobosa 2.0-2.5 mm longa. Sepala 5, crassiuscula concava quincuncialia 1.5-1.8 x 1.2-1.3 mm (in gemma), elliptica apice rotundata margine anguste hyalina ciliataque, abaxiale densiuscule hirtula, inferne coalita; pili unicellulares acuti hyalini. Petala 5, praeffloratione imbricata, 2.1-2.3 mm longa (in gemma), crassiuscula, elliptica obtusa concava, dorso linea mediali hirtula reliqua glaberrima, margine anguste hyalina et laevi. Stamina 20, filamentis basi connatis, parte libera filiformis glabris, quinque longioribus. Antherae 20 in alabastro adpresse 3-seriatae, connectivo crasso in 5 distalibus conniventibus acuto, thecis in torsis supra basim lateralibus. Discus non vidi. Ovarium ovatum 5-sulcatum glabrum, 5 septatum loculis uniovulatis. Stylus crassiusculus valde brevis. Stigma discoideum 5 lobulatum glutinosum, lobis cum 5 connectivis antherarum adpresse conniventibus alternantibus.

Humiriastrum liesneri is an interesting species distinguished by the rather small, obovate, subsessile, crenulate leaves, straight, upright leafy branches, and terminal, erect panicles. The flower is only known in bud stage. It is important to try to collect mature flowers, in full anthesis, to clear some significant features, among others, the structure of the anthers, in order to clarify the true relationships of the species. Its distinguishing characters from the other Venezuelan species are being keyed in the forthcoming flora of the Venezuelan Guayana.

FORMAL CORRECTION OF TWO SPECIFIC EPITHETS IN THE SOUTHERN CALIFORNIA FLORA

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ABSTRACT

Two specific epithets for southern California taxa, *Aster.greatai* S.B. Parish and *Salvia greatai* T.S. Brandegee, are formally corrected to proper Latin form in accordance with recommendations of the *International Code of Botanical Nomenclature*, 1988. The corrected spellings are *Aster greatae* Parish and *Salvia greatae* Brandegee.

KEY WORDS: *Aster*, *Salvia*, Asteraceae, Lamiaceae, nomenclature, southern California

In 1902, Samuel B. Parish named a newly discovered *Aster* species in honor of Mr. Louis A. Greata, a resident of San Francisco and an avid amateur plant collector. In so doing, Parish published the species with the epithet *Greatai*, apparently latinizing Greata's name implicitly to "Greataus" and consequently forming the genitive case, or possessive form, as "Greatai." Parish may have made this difficult construction under the false impression that a name or substantive terminating in *-a* in Latin or latinized form was exclusively of feminine gender; consequently, he chose the inopportune *-i* ending to express masculine genitive form. However, the Latin nouns of the first declension which end in *-a* in the nominative singular, while most often understood as being of the feminine gender, are not exclusively so. Examples in Latin include *poeta*, *poetae* (masculine - a poet, or "maker") and *agricola*, *agricolae* (masculine - a farmer, or "one who tills"). The genitive form of the name Greata, therefore, already being of proper Latin form as a first declension noun, is correctly constructed as *Greatae*.

William Stearn (1991) cites numerous analogous examples of this construction from European botanical literature; among them *Colchicum bivonae* Gussone, commemorating Antonino Bivona-Bernardi (1774-1837); *Doronicum*

columnae Tenore, for Fabio Colonna [Fabius Columna] (c. 1567-1650); and *Cirsium lacaitae* Petrak, honoring Charles Carmichael Lacaita (1853-1933). He goes on to state that "more than a hundred specific names with the epithet *balansae* commemorate the French botanical explorer Benedict Balansa (1825-1891) as a result of his extensive collecting. . . , thus Samuel Parish would undoubtedly have used the epithet *greatae* had he been better acquainted with European botanical literature and with botanical Latin."

A formal correction of the erroneously constructed and anomalous epithet, *greatai*, is hereby made in accordance with Article 73.10 and Recommendation 73C.1 of the *International Code of Botanical Nomenclature* (ICBN) adopted by the Fourteenth International Botanical Congress at Berlin, July-August 1987.

Aster greatae S.B. Parish, *nomen corrigendum*. Corrected from: *Aster Greatai* S.B. Parish, Bull. S. California Acad. 1:15, fig. 2. 1902. Type collection: *L.A. Greata s.n.*, Sept 1900. "Canyons of the San Gabriel Mts., near Pasadena."

Four years after Parish named his *Aster* in Louis Greata's honor, Townshend S. Brandegees named a newly discovered *Salvia* species in Greata's honor. Perhaps following the orthographic precedent established by Parish with his *Aster* taxon, Brandegees applied the epithet "*Greatai*" to this new *Salvia*.

Again, for the reasons already discussed above, this incorrectly constructed epithet is hereby corrected in accordance with the ICBN.

Salvia greatae T.S. Brandegees, *nomen corrigendum*. Corrected from: *Salvia Greatai* T.S. Brandegees, Zoe 5:229. 1906. Type collection: *H.M. Hall & L.A. Greata 5848*. "Cañon Springs wash, about four miles northeast of Dos Palmas, Riverside County, California."

FURTHER DISCUSSION

Both of the taxa dealt with here are relatively narrow endemics in southern California. *Aster greatae* ("Greata's Aster") is apparently limited to Los Angeles County, where it occurs in a few southerly canyons of the San Gabriel Mountains, as well as in the adjacent Verdugo Hills (a.k.a. "Verdugo Mountains"). It is currently on the California Native Plant Society's (CNPS's) List 4 (Plants of limited distribution - A watch list). *Salvia greatae* ("Orocopia Sage") is known from a limited area to the northeast of the Salton Sea in Riverside and Imperial counties. There is also an unconfirmed and debatable report from San Bernardino County. This species is currently on the CNPS's List 1B (Plants rare, threatened or endangered in California and elsewhere).

In the intervening years since these taxa were first published, the unusual orthography has caused a degree of confusion for members of the botanical community in southern California. A few workers, being aware of the orthographic problem, have used the correct Latin spellings in their works: e.g., *Aster Greatae* (Abrams 1904; Munz 1935) or *A. greatae* (Abrams 1917), and *Salvia Greatae* (Jaeger 1941; Munz 1935; Munz & Keck 1959) or *S. greatae* (Jepson 1943). Other workers, however, have chosen to retain the orthography as originally published: e.g., *A. Greatai* (Davidson & Moxley 1923; Munz & Keck 1959) or *A. greatai* (Abrams & Ferris 1960; Jepson 1923-25; Munz 1974; Smith & Berg 1988) and *S. greatai* (Abrams 1951; Jepson 1923-25; Munz 1974; Smith & Berg 1988). It is also apparent here that some authors have been inconsistent in their usage, favoring one name over another in subsequent publications.

The fact that these epithets have appeared in print under both spellings has only served to compound the nomenclatural confusion. There are also several floristic and botanical projects currently underway in California that will cite these species once again. A floristic treatment for Los Angeles County (the author, RSA), a floristic treatment for Riverside County (Steve Boyd, RSA), The Jepson Manual project related to the California flora (Dieter Wilken, Project Manager, JEPS), and the Fifth Edition of the California Native Plant Society's Inventory of Rare and Endangered Vascular Plants of California (CNPS, at Sacramento) may benefit from clarification of these taxon names.

In order to avoid continued confusion, and insofar as the specific epithets, as originally published, are contrary to the requirements of the ICBN, it is recommended that the corrected orthography formally presented herein be adopted henceforth.

ACKNOWLEDGMENTS

I express my thanks to Dr. William T. Stearn (K) and Dr. David M. Thompson (RSA) for reviewing this brief note, and to Annette H. Ross for helpful comments on the original manuscript.

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NOTES ON *AGERATINA* AND A NEW SPECIES OF *BARTLETTINA*
(EUPATORIEAE: ASTERACEAE)

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ABSTRACT

Corrections are noted in the recent key to *Ageratina* in Mesoamerica. These include the presence of *A. glauca* (Schultz-Bip. ex Klatt) R.M. King & H. Robinson in Guatemala, the identity of *A. motozintlensis* R.M. King & H. Robinson with *A. zunilana* (Standl. & Steyererm.) R.M. King & H. Robinson, and *A. thomasii* R.M. King & H. Robinson with *Eupatorium saxorum* Standl. & Steyererm., which is transferred here to *Ageratina*. *Bartlettina ornata* is described as new from Guatemala and Chiapas.

KEY WORDS: *Ageratina*, *Bartlettina*, Eupatorieae, Asteraceae, Mesoamerica

The recent paper on *Ageratina* in Mesoamerica (Robinson 1990) proves to have a number of errors including one inserted in press and some changes based on subsequent information. These changes can be corrected in copies of the text and key as indicated below. One change involves the need for the following new combination.

Ageratina saxorum (Standl. & Steyererm.) R.M. King & H. Robinson, *comb. nov.* BASIONYM: *Eupatorium saxorum* Standl. & Steyererm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23:182. 1944. HOLOTYPE: GUATEMALA. San Marcos: *Steyermark 36075* (F). *Fleischmannia saxorum* (Standl. & Steyererm.) R.M. King & H. Robinson, *Phytologia* 49:5. 1981.

Ageratina thomasii R.M. King & H. Robinson, *Phytologia* 69:73. 1990.
HOLOTYPE: MÉXICO. Chiapas: *Croat 47279* (US).

The species has been erroneously considered a *Fleischmannia* in previous studies by the authors (King & Robinson 1987, p. 289, 530, 538). The species runs in the recent key to Mesoamerican *Ageratina* to *A. thomasi* of Chiapas (Robinson 1990), which is treated here as a synonym. The *Ageratina* paper also has four other errors. The key shows a flaw inserted in press in placement of the second half of couplet 7, which should be located after couplet 16, rather than after couplet 10. The legend for *Ageratina subcoriacea* R.M. King & H. Robinson should be corrected to show the repository as DS rather than US. The latter is correct in the text. Other changes can be noted for anyone wishing to annotate the key. The author accepts the conclusion of B.L. Turner, who has annotated the type of *Ageratina motozintlensis* R.M. King & H. Robinson as *A. zunilana* (Standl. & Steyerf.) R.M. King & H. Robinson. The differences in sizes of many parts of the plants do not seem taxonomically important. Added to the flora is *Ageratina glauca* (Schultz-Bip. ex Klatt) R.M. King & H. Robinson, which would key close to *A. pringlei* (B.L. Robinson & Greenm.) R.M. King & H. Robinson. The two differ respectively by the petioles being 0.1-0.3 cm long, the leaf blades being elliptic-ovate, and the inflorescence being corymbose versus the petioles being 0.5-2.0 cm long, the leaf blades being deltoid, and the inflorescence being thyrsoid.

A review of the genus *Bartlettina* in Mesoamerica shows the need to recognize the following undescribed species.

Bartlettina ornata R.M. King & H. Robinson, *sp. nov.* HOLOTYPE: GUATEMALA. Chimaltenango: Chichavac; alt. 2400-2700 m. Shrub with wand-like stems about 8 ft high. Flowers purple. Growing in a shady ravine beside a stream. Rare. "Chichavac." March 1, 1933. *Skutch 304* (US). PARATYPES: MÉXICO. Chiapas: Along road between Motozintla de Mendoza and Siltepec, 26-30 miles N of Motozintla 9.5-4.5 miles S of Siltepec; disturbed primary forest; elev. 1000-1300 m. 1.5 m; flowers white. 12 Feb. 1979. *Croat 47454* (MO,US); 21.5 miles NW of Motozintla; 1.3 miles E of El Porvenir; disturbed primary cloud forest; elev. 1770 m. Shrub 3 m; flowers lavender. 11 Feb. 1979. *Croat 47339* (MO,US); Municipio of Motozintla de Mendoza, along the road from Huixtla to El Porvenir and Siltepec, on the north and west slope of Cerro Mozotal below the microwave tower, steep slope, evergreen cloud forest with *Quercus*, *Pinus*, *Abies*, *Drimys*, *Photinia*, *Clethra*, *Cornus*, and *Symplocos*; elev. 3000 m. Flowers lavender; shrub 10 feet tall. 30 December 1972. *Breedlove & Thorne 31188* (CAS,US); Along hwy. Mex. 190, 10 km SW of Motozintla. 15° 20' N, 92° 17' W; deciduous forest in ravine, with *Carpinus caroliniana* dominant, *Hedyosmum mexicanum*, *Sechium compositum*, *Quercus*; alt. 1725 m. 1 m tall; inflorescence pale purplish; flowers odorless. 24 Dec. 1985. *Nee & Andres 32325* (NY,US,XAL); Municipio of Union Juárez, on SE side of Volcán Tacaná,

steep slopes with montane rain forest, *Quercus*, *Pinus*, *Billia*, *Turpinia*, *Saurauia*, *Ostrya*, *Dendropanax*, and *Nectandra*; elev. 2200 m. Flowers lavender. 23 November 1980. *Breedlove & Almeda 47719* (CAS,US).

GUATEMALA. Dept. unknown: Inter Sta. (illegible) et Sta. Lucia. Jan. 1878. *Bernoulli & Cario 1449* (GOET). Chimaltenango: Between Los Idolos and Los Chocoyos, road to Panajachel, common in wet thicket along river, alt. 2400 m. Flowers lilac; shrub 3 m. Jan. 15, 1966. *Molina, Burger, & Wallenta 16212* (F); Barranca Los Chocoyos, near Idolos bridge about 5 km W of Patzún, Sierra Madre Mountains; alt. 2000 m. Flowers purple; shrub (weak) 2 m tall. Dec. 21, 1972. *Williams, Molina, & Williams 41560* (F); Calderas. Oct. 25, 1937. *Johnston 1115* (F); Slopes of Volcán de Acatenango, above Las Calderas, in dense wet *Chiranthodendron* forest, alt. 2400-2700 m. Jan. 3, 1939. *Standley 61814, 61950* (F); Quisaché, in a moist forested barranca; alt. 1800 m. Jan. 5, 6, 1939. *Standley 62024* (F). Jalapa: Sierra Miramundo, above Mataquescuintla, cloud forest; alt. 2800 m. Herb 1 m. Feb. 13, 1949. *Williams & Molina 15526* (F). Quezaltenango: Aguas Amargas, on the western slope of Volcán de Zunil, wet hillside forest; alt. c. 2450 m. Shrub 2 m tall, heads purple. Jan. 14, 1941. *Standley 83963* (F); Volcán de Zunil, at and above Aguas Amargas, moist forest; alt. 2430-2850 m. Shrub 6 ft.; heads pale purple. Feb. 17, 1939. *Standley 65438* (F); Volcán Santa María; alt. 8000-11500 ft. Jan. 24, 1896. *Nelson 3718* (US); Volcán Santo Tomás; alt. 2500-3700 m. "flor celeste" Shrubby, 8-10 ft.; flowers lilac, involucre pale green; leaves membranaceous, dark grass-green above, pale green beneath with a gray pubescence on midrib. Jan. 22, 1940. *Steyermark 34705* (F); "flor de rosa" Shrubby, 8-12 ft. tall; flowers lilac; leaves regular, similar in shape throughout. Jan. 22, 1940. *Steyermark 34717* (F). Quiché: 1942. *Aquilar 971* (F). Sacatepéquez: trail above La Cumbre de Calderas (radio towers, W of San Miguel Dueñas, 2 km W of San Juan Calderas); lower forest. Spindly shrub, 2-3 m tall; flowers purplish. Oct. 23, 1990. *Norrbom 90G-27* (US); Acatenango. Feb. 20, 1905. *Kellerman 4988* (US); Nacimiento del Cangrejal, Cuesta de Las Cañas, colinas humedas; alt. 1650 m. Fls. moradas; arbusto 2 m. Feb. 3, 1949. *Molina 15445* (EAP,US); Cuesta de la Cañas, above Antigua, damp thicket; alt. c. 1950 m. Shrub 10 ft.; buds only. Dec. 6, 1938. *Standley 58951* (F); Volcán de Agua; alt. 9000 pp. Apr. 1890. *J.D. Smith 2326* (F,US); Slopes of Volcán de Agua, above Santa María de Jesús, damp forest; alt. 2250-3000 m. Feb. 11, 1939. *Standley 65092* (F). San Marcos: Mountains along the road between San Marcos and Serchil, dense *Abies-Cupressus* forest; alt. 2700-3150 m. Shrub 2 m tall; flowers purple. Jan. 30, 1941. *Standley 85384* (F); Puente de Nahuatl-aa, near San Marcos; damp ravine, alt. c. 2280 m. Shrub 5 ft.; heads

pale purple. Feb. 22, 1939. *Standley 66290* (F); Río Vega, near San Rafael and Guatemala-México boundary, Volcán Tacaná; alt. 2500-3000 m. Shrub 8 ft. tall. Feb. 20, 1940. *Steyermark 36222* (F); between San Rafael Pie de la Cuesta and Palo Gordo, west-facing slope of the Sierra Madre Mountains, wet mountain forest near Aldea Fraternidad; alt. 1800-2400 m. Shrub 4 m high. Dec. 10-18, 1963. *Williams, Molina, & Williams 25768* (F,US); Cerro Tumbador, Sierra Madre Mountains, about 15 km W of San Marcos, ravines in mixed forest on slopes; alt. 2600 m. Flowers pink; shrub 6 m tall. Dec. 15, 1962. *Williams, Molina, & Williams 23088* (F); Along road between San Sebastián at km 21 and km 8, 8-18 miles NW of San Marcos, shaded slopes at base of cliff; alt. 2700-3800 m. Shrub 10 ft. tall; flowers lavender. Feb. 15, 1940. *Steyermark 35747* (F); Volcán Tajumulco, between Las Canoas and top of ridge, 7 mi. from San Sebastián, upper south-facing slopes; alt. 3300-3900 m. Feb. 16, 1940. *Steyermark 35852* (F); Tajumulco Volcán, Sierra Madre Mountains about 8-10 km W of San Marcos, montane cloud forest area on outer slopes; alt. ca. 2300 m. Herb 1 m tall. Dec. 31, 1964-Jan. 1, 1965. *Williams, Molina, Williams, Gibson, & Laskowski 26850* (F); In forest; alt. 2400-2700 m. Flowers lilac; 1 m tall. Jan. 3, 1965. *27204* (F); Vicinity of town of Tajumulco, NW slopes of Volcán Tajumulco, slopes of barranca; alt. 2300-2800 m. Shrubby 3-5 ft. tall, leaves dark green above, paler beneath, membranaceous. Feb. 28, 1940. *Steyermark 36865* (F); Road to Tajumulco Volcano, Sierra Madre Mountains, near San Andrés, montane cloud forest, in forest; alt. 2900 m. Tree 5 m tall; heads light pink. Jan. 2, 1965. *Williams, Molina, Williams, Gibson, & Laskowski 27045* (F). Sololá: Volcán Atitlán. Feb. 16, 1906. *Kellerman 5357* (US); Volcán Atitlán, 8000 ft., Jan. 23, 1907. *Kellerman 6288* (F); Volcán Tolimán (side facing Volcán Atitlán to summit); alt. 2700-3100 m. Shrub 20 ft. tall. June 13, 1942. *Steyermark 47588* (F); Near Nahuala, Sierra Madre Mountains, ravines, alt. 2500 m. Flowers pale purple; shrub 5 m tall. Dec. 17, 1962. *Williams, Molina, & Williams 23180* (F).

Plantae fruticosae ad 3 m altae mediocriter ramosae; caules fistulosi vel non fistulosi brunnescentes interdum evanescentiter puberuli. Folia opposita, petiolis plerumque 1.5-6.0 cm longis; laminae late ovatae vel subrhomboidae plerumque 5-16 cm longae et 4-16 cm latae in tertiam inferioriam latissimae base obtusae margine argute acutae saepe in partibus latissimis valde dentatae vel acuminate angulatae apice breviter vel anguste acuminatae in superficiis sparse puberulae vel subglabrae subtus minute glandulopunctatae ex 5-20 mm supra basem leniter trinervatae. Inflorescentiae pyramidaliter paniculatae; bractee in nodis inferioribus

2-3 foliiformes. Capitula c. 7 mm alta; bractee involucri 16-18 anguste oblongae 4-5 mm longae c. 1 mm latae apice scariosae anguste rotundatae; receptacula breviter vel longe spinulifera. Flores 5-12; corollae plerumque lavandulae 4.0-4.5 mm longae, tubis 2.0-2.5 mm longis, faucibus c. 2 mm longis, lobis c. 0.4 mm longis et 0.5 mm latis extus puberulis; appendices antherarum subgradratae c. 0.2 mm longae et latae. Achaenia c. 2 mm longa glabra; setae pappi 3-4 mm longae apice mediocriter attenuatae.

The new species is represented by many specimens that have been previously identified as *Bartlettina oresbia* (B.L. Robinson) R.M. King & H. Robinson, *B. oresbioides* (B.L. Robinson) R.M. King & H. Robinson, and *B. luzii* (B.L. Robinson) R.M. King & H. Robinson, and more recently as *B. breedlovei* R.M. King & H. Robinson and *B. hylobia* (B.L. Robinson) R.M. King & H. Robinson. The leaves commonly have lateral angles on the blades as in the former two species, but the heads have fewer than 20 florets as in the last species. Recent identity with *B. hylobia* has been mostly because of the reduced number of florets, but the latter species proves to be a rather local endemic in Chiapas, with strictly ovate leaf blades and 14-20 florets in each head. The new species is distinct from all others by the heads with 5-12 florets and by the spinose receptacle. The receptacular spines vary from short and crested to lacinate and are half as long as the achenes. The spines are actually sclerified receptacular outgrowths, rather than hairs of the type common in the subtribe Hebeclininae.

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NEW SPECIES AND NEW COMBINATIONS OF CRITONIINAE FROM
MESOAMERICA (EUPATORIEAE: ASTERACEAE)

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ABSTRACT

Koanophyllon jinotegense R.M. King & H. Robinson is described as new from Nicaragua, *Eupatorium siltepecanum* B. Turner is transferred to *Critonia*, *Eupatorium heathiae* B. Turner is transferred to *Adenocritonia*, and *A. steyermarkii* is described as new. A key is provided for the three species of *Adenocritonia*.

KEY WORDS: *Koanophyllon*, *Adenocritonia*, *Critonia*, Eupatorieae, Asteraceae, Mesoamerica

A review of the Mesoamerican species of *Koanophyllon* shows that a number of specimens from central Nicaragua represent a previously undescribed species. The description is as follows:

Koanophyllon jinotegense R.M. King & H. Robinson, *sp. nov.* HOLOTYPE: NICARAGUA. Jinotega: Along road from Hwy 3 to La Fundadora; ca. 13° 02-04' N, 85° 54-55' W, elev. 1200-1400 m; cafetales, pastures and patches of cloud forest; collected with O.M. Montiel. Tree 6 m tall. 9 Dec 1983. *W.D. Stevens 22543* (US; Isotypes: MO, TEX). PARATYPES: NICARAGUA. Jinotega: Same locality as holotype; collected with P. Moreno & R. Riviere. Tree ca. 8 m tall, heads white, 28 Sep. 1982, *W.D. Stevens 21852* (MO, US). Matagalpa: Cordillera Central de Nicaragua; Finca Santa María de Ostuma, wet montane cloud forest area, alt. 1300-1500 m. Tree to 8 m, in clearing. Nov. 30 - Dec. 4, 1973. *L.O. Williams & A. Molina R. 42694* (F, US); vicinity El Porvenir 4 km E of Santa María de Ostuma, common in clearing of forest, alt. 1500 m. Oct. 30, 1968. *A. Molina R. 22884* (F, US).

Plantae frutescentes et arborescentes 3-8 m altae mediocriter ramosae; caules teretes dense patentiter pilosuli vel hirtelli. Folia opposita, petiolis 0.5-2.5 cm longis hirtellis; laminae herbaceae ellipticae plerumque 10-17 cm longae 2.5-4.5 cm latae base breviter acuminatae margine serratae apice anguste acuminatae supra et subtus plerumque glabrae in nervis tenuiter puberulae subtus interdum fere ad nervam puberuliores, nervis secundariis pinnatis utrinque 4-5, nervis basilaribus ad marginem mediocriter conniventibus. Inflorescentiae late pyramidaliter paniculatae, ramis patentibus dense pyramidalibus. Capitula 5-6 mm alta; involucrium ca. 3.5-4.5 mm longum; bracteae involucri ca. 12 ovatae vel oblongo-lanceolatae plerumque 2.0-4.5 mm longae 0.8-1.2 mm latae breviter acutae. Flores 15-16; corollae albae 2.5-3.3 mm longae, tubis 0.8-1.0 mm longis, faucibus 1.7-2.0 mm longis, lobis ca. 0.7 mm longis et 0.6 mm latis; thecae antherarum ca. 1 mm longae; appendices antherarum breves duplo latiores quam longiores. Achaenia ca. 2 mm longa in superficiis superne tenuiter setulifera; setae pappi 2.5-3.0 mm longae in latitudo uniformes.

Specimens of the new species have been previously identified as the species now known as *Koanophyllon hylonomum* (B.L. Robins.) R.M. King & H. Robinson and *K. pittieri* (Klatt) R.M. King & H. Robinson, but both of the latter differ by the puberulous rather than pilose or hirtellous pubescence of stems and inflorescence branches, and by the shorter, obtuse or round tipped rather than longer acute tipped involucrial bracts.

Two Chiapas species of *Eupatorium* recently described by Turner (1990) both show characters of *Critonia* mixed with features normally found in other genera. One of the species clearly falls within *Critonia*, but it has many floral features of *Bartlettina*. The mixture looks like it might be the result of intergeneric hybridization of the type suggested for other elements of the tribe (King & Robinson 1987, p. 11). The second species has more of the general aspect of a *Critonia*, but it has glandular punctations on the leaves more like *Koanophyllon* or *Chromolaena*. It is placed here in *Adenocritonia* along with a new species from Guatemala. The new combinations and description are as follows:

Critonia siltepecana (B. Turner) R.M. King & H. Robinson, *comb. nov.*
 BASIONYM: *Eupatorium siltepecanum* B. Turner, *Phytologia* 69:123.
 1990. HOLOTYPE: MÉXICO. Chiapas: near Siltepec, *Matuda 5156* (LL).

The leaves of the species have what Turner (1990) calls "pustulate blisters." These are well developed, internal vesicles of the type found in the tribe only in *Critonia*. The species is more pubescent than most species of *Critonia* but falls

fully within the overall variation of pubescence found in the genus. The species has short, crowded heads, small involucral bracts, funnelform corolla limbs, and puberulous corolla lobes with 1-2 glandular dots that give the superficial appearance of a *Bartlettina* rather than a *Critonia*, and it has a few hairs on the receptacle and some unusual mammilosity on the style branches. Nevertheless, there are no unquestionable characters of the subtribe Hebeclininae to which *Bartlettina* belongs. The hairs on the receptacle are fewer and coarser than those found in the Hebeclininae, and the achene base is totally Critoniinae.

The species can be placed in the recent key to Mesoamerican *Critonia* (Robinson 1990) before couplet 10. At that point the species can be distinguished by the densely puberulous stems versus pilose or glabrous stems, heads ca. 5 mm long versus 6-15 mm long, funnelform versus tubular corolla limbs, and the puberulous versus mostly glabrous corolla lobes. The internal vesicles of the leaves are mostly rounded as in the first group under couplet 10, and the heads are essentially sessile as in the second group of couplet 10. The leaf venation is pinnate, but the secondary veins are ascending at angles of ca. 45°.

Adenocritonia heathiae (B. Turner) H. Robinson, *comb. nov.* BASIONYM: *Eupatorium heathiae* B. Turner, *Phytologia* 69:122. 1990. HOLOTYPE: MEXICO. Chiapas: Mapastepec, *Heath & Long 1128* (TEX!).

Adenocritonia heathiae is discussed below under the following new species.

Adenocritonia steyermarkii H. Robinson, *sp. nov.* HOLOTYPE: GUATEMALA. San Marcos: Between La Vega ridge along Río Vega and NE slopes of Volcán Tacaná, to 3 miles from Guatemala-México boundary, in vicinity of San Rafael, along stream; alt. 2500-3000 m. Shrub 10 ft. tall; corolla lilac; leaves dull green, sticky, subcoriaceous. Feb. 20, 1940. *Steyermark 36183* (F). PARATYPES: GUATEMALA. Quezaltenango: Region of Boxantín, southeast of San Martín Chile Verde, wet sandy quebrada; alt. about 2400 m. Shrub 2 m tall; heads pinkish. Jan. 18, 1941. *Standley 83777* (F); Mountains southeast of Palestina, on old road to San Juan Ostuncalco, damp mixed hillside forest; alt. 2550-2850 m. Jan. 21, 1941. *Standley 84223* (F).

Plantae fruticosae ad 2.5 m altae mediocriter ramosae; caules pallide fulvi evanescentiter puberuli. Folia opposita, petiolis 2-5 cm longis; laminae ovatae plerumque 7-15 cm longae et 3.5-10.0 cm latae base obtusae vel subacutae margine dense serratae apice acutae vel vix acuminatae supra et subtus sparse glandulopunctatae supra puberulae et densius puberulae in nervis primariis subtus in nervis et nervulis puberulae, nervis secundariis ascendentiter subpinnatis prope basim tenuibus et ad marginem subparallelibus vel conniventibus, nervis secundariis validissimis prope

quaternis inferioribus leniter trinervatis. Inflorescentiae in ramis foliiferis terminales subpyramidales 12-16 cm altae et 9-12 cm latae, ramis dense corymbosis, ramulis ultimis 0.5 mm longis dense puberulis. Capitula c. 9 mm alta anguste campanulata; bracteae involucri substramineae 16-18 subimbricatae valde inaequales 3-4 seriatae interiorissimae facile deciduae omnes breviter oblongae vel lineari-oblongae plerumque 1.5-5.0 mm longae 1.0-1.5 mm latae apice rotundatae extus 3-striatae et puberulae; receptacula plana glabra. Flores 5 in capitulo; corollae lavandulae anguste infundibulares 6.0-6.5 mm longae, tubis c. 2.5 mm longis, faucibus c. 3 mm longis, lobis c. 0.5-0.7 mm longis utrinque laevibus extus glandulopunctatis; thecae antherarum c. 1.8 mm longae; appendices antherarum oblongo-ovatae c. 0.40-0.45 mm longae et c. 0.3 mm latae; appendices stylorum anguste spathulatae. Achaenia prismatica 5-costata c. 3.5 mm longa dense minute glandulifera in costis interdum minute puberula non setulifera; setae pappi albae c. 40 plerumque 3.5-4.5 mm longae apice tenuiores.

The two species have the aspect of a *Critonia* but have glandular punctations on the leaves. The combination of characters readily places the species in *Adenocritonia*. The latter genus has been known from a single Jamaican species, *A. adamsii* R.M. King & H. Robinson. *Adenocritonia* has been noted (King & Robinson 1987, p. 302, 303) for the shorter anther appendage of its type species. The length of the anther appendage is useful for separating various other genera such as *Critonia* and *Critoniadelphus*, but the longer appendage of the Chiapas species and the new species are not considered here as adequate reason to make a generic distinction between them and *Adenocritonia* of Jamaica. Besides the anther appendage difference, the Jamaican species has more attenuate bases on the leaf blades, more numerous basal bracts of the involucre, more stramineous and less striated involucre bracts, and achene surfaces with a few glands rather than short setulae or many small glands. The new species is individually distinctive in the short tips of its leaves, the width of its stems and leaves, and the size of its marginal teeth, its heads, and its glanduliferous achenes. Specimens of the new species had previously been identified as *Eupatorium luxii* B.L. Robinson and *E. oresbioides* B.L. Robinson, species belonging to the remotely related genus *Bartlettina*. The three species may be distinguished as follows.

1. Anther appendages half as long as wide; involucre with 3-5 series of congested minute bracts at base, inner bracts with scarcely depressed striations, with depressed glandular punctations; leaf bases and tips narrowly acuminate, upper surfaces of midveins subglabrous. *A. adamsii*

1. Anther appendages as long as wide or longer; involucre with only a few isolated minute bracts at base, inner bracts with three distinctly depressed striations, without obvious depressed glandular punctations; leaf bases obtuse to short acute, not or scarcely acuminate, upper surfaces of midveins distinctly puberulous.
2. Leaf apices narrowly acuminate, leaf margins crenulate-serrulate; heads c. 6 mm high, with 4 florets; achenes c. 2 mm long, with distinct setulae on ribs and upper sides, without glands.
 *A. heathiae*
2. Leaf apices acute or shortly acuminate, leaf margins closely and coarsely serrate; heads c. 9 mm high, with 5 florets; achenes c. 3.5 mm long, without distinct setulae, with numerous minute glands on surface. *A. steyermarkii*

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**TWO NEW SPECIES OF *FLEISCHMANNIA* FROM MESOAMERICA
(EUPATORIEAE: ASTERACEAE)**

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ABSTRACT

Fleischmannia suderifica R.M. King & H. Robinson and ***F. yucatanensis*** R.M. King & H. Robinson are described as new from Guatemala and Yucatán respectively.

KEY WORDS: Asteraceae, Eupatorieae, *Fleischmannia*, Mesoamerica

A study of the genus *Fleischmannia* in Mesoamerica has resulted in recognition of 31 species from the area, of which the following two are previously undescribed.

Fleischmannia suderifica R.M. King & H. Robinson, *sp. nov.* HOLOTYPE: GUATEMALA. Izabal: Cristina, Dryish ditch along railroad. Secondary shoots. Leaves used for a sudorific tea. Nom. vernac. "te'." 22 May 1919. *Blake 7576* (US).

Plantae herbaceae perennes c. 0.4 m altae; caules pallide brunnescentes breviter puberuli non fistulosi. Folia opposita, petiolis 3-6 mm longis; laminae oblongo-ovatae plerumque 2.3-3.3 cm longae 6-14 mm latae base breviter acutae trinervatae margine superne pauce crenulato-serrulatae apice anguste rotundatae supra puberulae subtus in nervis et in superficiis plerumque glabrae non vel obscure glandulo-punctatae. Inflorescentiae corymbosae c. 5 cm latae et 3-4 cm altae, ramulis in glomerulis paucis subdensis dispositis, pedunculis 1-4 mm longis puberulis. Capitula 4-5 mm alta; bracteae involucri c. 22 subimbricatae basiliores plerumque dense insertae plerumque anguste oblongae 1.0-3.5 mm longae 0.5-0.7 mm latae apice obtusae margine anguste scariosae extus minute pilosulae. Flores c. 30 in capitulo; corollae lavandulae c. 2 mm longae,

lobis c. 0.3 mm longis breviter puberulis; rami stylosum anguste lineares. Achaenia c. 1.3 mm longa superne in costis pauci-setulifera, costis persistentiter flavis; setae pappi c. 22 c. 2 mm longae base contiguae.

Fleischmannia suderifica most closely resembles *F. crocodilia* in its blunt, oblong leaves having essentially glabrous undersurfaces, but the latter has only c. 15 flowers in the heads and has glabrous achenes without persistently yellow ribs. The specimen is labeled as being of secondary shoots, but there is no reason to assume that any characters of the heads would be altered in such shoots. The achenes of the new species combine the persistently yellow ribs of the *F. pycnocephala* (Less.) R.M. King & H. Robinson type with the contiguous bases of pappus bristles of the *F. pratensis* (Klatt) R.M. King & H. Robinson type.

Blake's collection label mentions that leaves were used in the area for a sudorific (diaphoretic) tea. The note is used as the basis for the species name, although it seems unlikely that the Guatemalan natives made a distinction between any of the closely related species in the area.

Fleischmannia yucatanensis R.M. King & H. Robinson, *sp. nov.* HOLOTYPE: MÉXICO. Yucatán: Xnocac. Dec. 1916. *Geo. F. Gaumer & sons 23501* (US 1267807). PARATYPE: Yucatán: 1917-1921. *Geo. F. Gaumer 23501* (US 1267806).

Plantae herbaceae perennae ad 0.8 m altae; caules flavescentes minute puberuli non fistulosi. Folia opposita, petiolis 0.5-0.7 cm longis; laminae ovatae plerumque 1.8-2.5 cm longae 0.8-1.4 cm latae base breviter obtusae trinervatae margine in partibus medianis crenulatae apice acutae supra et subtus in nervis et superficiis minute et uniformiter puberulae subtus non vel obscure glandulopunctatae. Inflorescentiae thyrsoidae, ramis late patentibus laxe cymosis, pedunculis 3-7 mm longis minute puberulis. Capitula 4-5 mm alta; bracteae involucri 1.5-4.5 mm longae c. 0.8 mm latae, bracteae interiores obtusae late scariosae extus subglabrae. Flores c. 18 in capitulo; corollae albae c. 2.5 mm longae glabrae, lobis c. 0.3 mm longis; rami stylosum distaliter latiores. Achaenia c. 1.8 mm longa in costis persistentiter pallida superne et in costis minute scabridula; setae pappi c. 30 c. 2.5 mm longae base contiguae.

The two specimens seen of *Fleischmannia yucatanensis* have the same collection number but may not really be duplicates. The holotype is from Xnocac, collected by Gaumer & sons, and is dated Dec. 1916. The second specimen has no locality except Yucatán, is by only Geo. F. Gaumer, and is dated 1917-1921. The holotype was originally distributed from the Field Museum as *Eupatorium*

microstemon Cass., while the second specimen was distributed as *Coleosanthus diffusus* (Vahl) Kuntze. Both specimens have lax, thyrsoid inflorescences similar to those of *F. seleriana* (B.L. Robinson) R.M. King & H. Robinson (including *Eupatorium antiquorum* Standl. & Steyerl.) in general form, but the latter is much more robust and has densely hirsute stems and leaf surfaces. The dense, fine puberulence on the leaves of the new species resembles that of *F. deborabellae* R.M. King & H. Robinson. The latter species, of the mountains of Guatemala and Honduras, differs by its more robust form, its often denser inflorescence, its pale lavender corollas, and the numerous obvious glands on its leaf surfaces.

TWO NEW SPECIES OF *MIKANIA* IN MESOAMERICA (EUPATORIEAE:
ASTERACEAE)

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ABSTRACT

Mikania castroi R.M. King & H. Robinson is described from Costa Rica from material previously determined as *M. gonzalezii* B.L. Robinson & Greenman, and *Mikania verapazensis* R.M. King & H. Robinson is described as new from Guatemala.

KEY WORDS: *Mikania*, Eupatorieae, Asteraceae, Mesoamerica

Study of the genus *Mikania* for preparation of the Flora Mesoamericana treatment has shown the need for the description of the following two new species:

Mikania castroi R.M. King & H. Robinson, *sp. nov.* HOLOTYPE: COSTA RICA. Cartago: North and south slopes of ridge on E side of Río Grande de Orosi, opposite mouth of Río Humo, ca. 6 km upstream from Tapantí. Elev. ca. 1500-1800 m. 9° 43' N, 83° 47' W. Coarse vine fallen to ground in disturbed area in forest. Flowers white. Nov. 24, 1984. *M. Grayum*, *J. Beach*, & *P. Sleeper* 4540 (US; Isotype: MO). PARATYPES: COSTA RICA. Alajuela: Viento Fresco, alt. 1600-1900 m. Wet thicket; large herbaceous vine; flowers dirty white. Feb. 13, 1926. *P.C. Standley* & *R. Torres R.* 47791 (US). Heredia: Yerba Buena, NE of San Isidro, alt. about 2000 m. Wet thicket, large herbaceous vine, flowers dirty white. Feb. 22, 28, 1926. *P.C. Standley* & *J. Valerio* 50093 (US); Vara Blanca de Sarapiquí, N slope of Central Cordillera, between Poás and Barba volcanoes, alt. 1650 m. Edge of forest. Vine with clasping petioles, flowers white. March 1938. *A.F. Skutch* 3655 (US). Limón: Cordillera de Talamanca, headwaters of the unnamed western branch of the Río Teribe, between the Río Sini and the continental divide at Cerro Bekom; 9° 10' 45" N, 83° 03' 30" W; Elev. 2500-2600 m. Mixed oak forest along

river with a clearing of kikuyu pasture. Vine, florets white. March 21 & 27, 1984. *G. Davidse, G. Herrera Ch. & R.H. Warner 25784* (MO,US). Puntarenas: Monteverde, sendero Chomogo. Elev. 1500-1600 m. Liana en bosque secundario; flores blancas. Sept. 7, 1985. *W.A. Haber & E. Bello C. 2637* (MO,US). San José: along route 216, ca. 8 km generally N of Nubes. Elev. ca. 4900 ft. Uncommon vines up to 3 meters above ground, flowers grey-white. June 13, 1974. *R.M. King 6781* (US).

Plantae volubiles ad 3 m altae; caules subteretes glabri in nodis lateraliter non vel minute lobulati. Folia opposita, petiolis plerumque 2-7 cm longis; laminae ovatae 4.5-15.0 cm longae 1.5-9.0 cm latae base late rotundatae vel subcordatae margine integrae vel remote denticulatae apice anguste acuminatae supra et subtus glabrae fere ad basem valde ascendentiter trinervatae. Inflorescentiae in internodis elongatae flexuosae, ramis corymbosis, pedunculis 2-7 mm longis sparse minute puberulis. Capitula 8-9 mm alta; bractae subinvolucris ellipticae 3-5 mm longae 1.5-2.0 mm latae; bractae involucris oblongae 6-7 mm longae et 1.0-1.5 mm latae apice breviter acutae extus glabrae vel sparse minute puberulae. Corollae albae extus plerumque glabrae, tubis cylindraceis 2.5-3.0 mm longis, faucibus nullis, lobis anguste oblongis ca. 2 mm longis 0.3-0.4 mm latis inferne intus breviter dense papillois, nervis loborum marginatis; basi stylorum glabri; appendices stylorum dense breviter papillois. Achaenia ca. 3.5 mm longa glabra; setae pappi 4.5-5.0 mm longae vix scabridae apice non vel vix latiores.

The species is named for Victor Castro of the Universidad de Costa Rica, Escuela de Química, San José, Costa Rica. Specimens of the species have not previously been distinguished from *Mikania gonzalezii* B.L. Robinson & Greenman, which also occurs in Costa Rica. *Mikania gonzalezii* was originally described from México as having acute leaves with five nerves from the shallowly cordate blade bases. The latter species has been known from Costa Rica since a determination many years ago by S.F. Blake of an Austin Smith collection (*P2167*, US). It has been recently redescribed and illustrated, and recognized from Panamá and from additional Mexican collections by Holmes (1990). Distinctions of the new species from *M. gonzalezii* include the separation of the corolla lobes to the top of the basal tube, the veins of the lobe being close to the margin, the completely glabrous leaves and stem internodes, and the more weakly scabrid pappus bristles with tips not or scarcely broadened.

Mikania verapazensis R.M. King & H. Robinson, *sp. nov.* HOLOTYPE: GUATEMALA. Alta Verapaz: Mountains E of Tactic, on road to Tamahú, alt. 1500-1650 m; dense wet forest. Woody vine. April 9, 1939. *P.C. Standley 71313* (F).

Plantae volubiles ad 3 m? altae sparse ramosae; caules subteretes pilosi in nodis non lobulati. Folia opposita, petiolis plerumque 1-2 cm longis; laminae ovatae circa vel ultra $1\frac{1}{2}$ longiores quam latiores plerumque 6-9 cm longae 3-6 cm latae base late rotundatae margine remote mucrono-denticulatae apice anguste acuminatae subtus sparse pilosae e 1-2 mm supra basem trinervatae, nervis secundariis ad $\frac{1}{5}$ ultimis attingentibus. Inflorescentiae in internodis elongatae flexuosae, ramis corymbosis, pedunculis 2-7 mm longis puberulis. Capitula c. 9 mm alta; bracteae subinvolucris ellipticae 3-5 mm longae; bracteae involucris anguste oblongae acutae c. 7 mm longae 1.5 mm latae extus glabrae; corollae albae?, tubis c. 3.5 mm longis, limbis demum abrupte salverformibus, faucibus c. 0.5 mm longis, lobis oblongo-ovatis c. 1.5 mm longis, nervis lobarum e marginis remotis; basi stylorum glabri; rami stylorum dense breviter papilloso. Achaenia c. 3.5 mm longa in costis dense spinoso-papillosa inter costas sparse puberula; setae pappi c. 5 mm longae apice vix latiores et vix scabridulae.

The single specimen is in poor condition, but distinctions are nevertheless evident in the pilosity of the stem, the glabrous involucre bracts, the tips of the pappus bristles, and the salverform limb of the corolla. The species differs from both the closest relatives, *Mikania gonzalezii* and *M. petrina* Standley & Steyermark, by the thinner and less roughened tips of the pappus bristles. The new species is more pubescent than the nearly glabrous *M. gonzalezii* but is less pubescent than *M. petrina* which has larger heads and pubescent involucre bracts. The corolla limbs of both related species seem to be broadly campanulate rather than salverform at maturity.

LITERATURE CITED

- Holmes, W.C. 1990. The genus *Mikania* (Compositae - Eupatorieae) in Mexico. Sida, Bot. Misc. 5:1-45.

LEAF ANATOMY OF FOURTEEN SPECIES OF *CALAMAGROSTIS* SECTION
DEYEUXIA, SUBSECTION *STYLAGROSTIS* (POACEAE: POOIDEAE)
FROM THE ANDES OF SOUTH AMERICA

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ABSTRACT

A scanning electron microscope and light microscope survey of the leaf epidermal and anatomical features in selected species of *Calamagrostis* from the Andes of South America was made for two purposes: first, to investigate any similarities or differences that may exist in the general and internal structure of the leaf of different species; and second, to investigate any structures of the leaf that may be associated with the environmental factors in these high altitude grasses. Abundant variation was found in such characters as the number of vascular bundles, number of ribs, patterns of distribution of sclerenchyma, shape and distribution of silica bodies, shape and distribution of epidermal papillae, leaf cross sectional outline, accumulation of silica in papillae and prickly hairs, stomata number and distribution, hair length, and hair distribution. The species studied exhibit anatomical and morphological diversification, which appears to be correlated with environmental factors.

KEY WORDS: grass leaf, leaf anatomy, Poaceae, *Calamagrostis*

INTRODUCTION

The genus *Calamagrostis* Adams. (Poaceae: Pooideae) with about 250 species is distributed worldwide (Bjoerkman 1969; Chase & Niles 1962; Clayton & Renvoize 1986). Approximately 70 poorly known species are found in the paramo and puna of South America. Studies based on microcharacters have shown that *Calamagrostis* is rather artificial (Hilu & Wright 1982), not appearing as a discrete cluster in any of their cluster analyses for the Gramineae.

It has been accepted that the anatomy of the leaf blade is an essential ingredient for a satisfactory analysis of grass taxonomy. The first person who pointed out that leaf anatomy might be useful in grass systematics was Duval-Jouve (1875), who found differences in bulliform cell distribution among species of different tribes and described two basic types of anatomy for grasses.

Many characters seen in the transverse sections of leaves appear to be quite constant and can be used with confidence in identifying grasses (Ellis 1976, 1979; Prat 1936). Other characters such as leaf size may vary with the habitat of the plant, but the basic form is genetically controlled (Humphries & Wheeler 1963).

Metcalf (1960) described leaf anatomy for *Calamagrostis epigeios* (L.) Roth and *Deyeuxia quadriseta* Benth. He made a complete description, including leaf, stem, root, and geographical distribution for *C. epigeios*. For *D. quadriseta*, however, he described only the leaf epidermis and cross sectional anatomy. Tuerpe (1962) studied thirteen species of *Deyeuxia* in the province of Tucuman (Argentina). She considered two types of leaf anatomy:

1. having the bundles appressed to both lower and upper epidermis (e.g., *D. montevidensis* Nees, a species that grows in lower elevations [1000-2500 m]).

2. having their bundles isolated, few stomata, frequent epidermal hairs, and round silica bodies, (e.g., *D. eminens* Presl [*C. eminens* (Presl) Steud.], a species that grows at high altitudes [3000-5500 m]). According to Prat (1932, 1936), the anatomical characteristics of the *Calamagrostis* leaf resemble those of the Triticeae. Metcalf (1960), based on his epidermal and anatomical studies of *Calamagrostis* and *Deyeuxia*, stated that the leaf is typically festucoid.

Metcalf (1960) published the most comprehensive work describing the anatomy and epidermal characteristics for the entire grass family. He described the generic characters for *Deyeuxia* and *Calamagrostis* based on one species for each genus.

MATERIALS AND METHODS

Field collections and herbarium material were used for comparative studies of cross sectional leaf anatomy and epidermal characters. The leaf cross sections were cut from the midsection of the blade. Fully developed leaves from dried specimens were softened by soaking in Pohl's solution for seven days (Pohl 1965). After softening was complete, the leaf material was washed in tap water for fifteen minutes and then desilicified in a 10% aqueous hydrofluoric acid solution for nine days for paraffin sectioning. For further processing, the leaf pieces were rinsed in running water for three hours. Dehydration was accomplished in steps of 25%, 50%, 70%, 95% (two changes), and 100% (two changes) ethanol, with a minimum of one hour for each step.

Leaf samples to be embedded in paraffin were first stained in a solution of 1% safranin in 1:1 ethanol:xylene for one hour, and then passed through two changes of xylene before infiltration in melted wax (melting point 56.5 ° C) for one week. Sections were cut on a rotary microtome at 10 μ m thickness, and stained in safranin and fast green using standard procedures (Berlyn & Miksche 1976; Sass 1958). Living leaf blades were cut in water and stained following the procedure for making permanent free hand cross sections (cover slip was sealed using two coats of clear nail polish).

For scanning electron microscope (SEM) observations, the leaf epidermis and floret samples were selected under a binocular microscope. Leaf samples were selected by cutting square or rectangular sections from the midposition of mature foliage leaves. Complete florets and leaf samples were mounted on brass discs with silver paste or silver tape, coated with Au/Pd in a Polaron E5100 sputter coater, and viewed at 15 and 39 Kv in a Jeol JSM-35 Scanning Electron Microscope. To observe features such as silica bodies, cork cells, stomata, bulliform cells, and papillae more clearly, leaf sections were sonicated in xylene for 12-15 minutes to remove the epicuticular wax, then allowed to air dry before mounting. Photographs were taken using Polaroid type 665 positive/negative film. Elemental X-ray analysis for silicon was performed using a Kevex-ray subsystem 5000A X-ray energy spectrometer attached to the scanning electron microscope. Special observation of the adaxial epidermis under the scanning microscope was made for those specimens showing considerable contrast differences (deep furrows and elongated ribs) on the adaxial epidermis, by using "gamma control unit" to optimize the image contrast by decreasing the contrast in high contrasted areas (ribs) and increasing the contrast in low areas (furrows) (Horner & Elsner 1981).

RESULTS AND DISCUSSION

Anatomical description: subsection *Stylagrostis*. Leaf thickness was measured in various units or ribs with an average thickness of 0.5-1.0 mm. Transverse sections in normally permanently or temporarily infolded leaves exhibit reduced V shaped, U shaped, or round outline (Figs. 1e, 1f, 1g, 1h, 1i, 1j, 1k, 1l, 1m, and 1n). *Adaxial furrows*: from slight, shallow to deep, varying in shape from wide to narrow, and distributed between the vascular bundles. *Adaxial ribs or units*: situated over the vascular bundles with flat tops as in *Calamagrostis pisinna* Swallen (Fig. 7); rounded tops alternating with triangular tops as in *C. ampliflora* Tovar (Fig. 5); triangular tops as in *C. ovata* (Presl) Steud. (Fig. 6). *Abaxial furrows and ribs*: not present. *Median vascular bundle*: present but sometimes not distinguishable from other primary vascular bundles. Usually the leaf infolding occurs in the medial furrow or rib with no structurally distinct midrib projecting abaxially (Fig. 1). Frequently, the central primary vascular bundle is surrounded by a large group of

parenchyma (Fig. 7) or thick walled cells (Fig. 5) and/or sclerenchyma (Figs. 2 and 7). *Vascular bundle arrangement*: first order vascular bundles present, varying in number. The xylem of first order vascular bundles is characterized by large metaxylem vessels on either side of the protoxylem (Figs. 2 and 3). The vascular bundles may be circular (Fig. 7), ovate (Fig. 5), or apple shaped (Fig. 3). The phloem is sometimes sclerosed, connected or not to lignified fibers. *Second order vascular bundles*: usually present, round or ovate, xylem and phloem, well differentiated, sometimes the same size as first order vascular bundles but lacking large metaxylem vessels. *Third order vascular bundles*: sometimes present, mostly bearing phloem and lacking bundle sheaths. *Vascular bundle sheaths*: a double vascular sheath surrounding each vascular bundle, not distinguishable in third order vascular bundles. The outer or parenchyma sheath cells are well differentiated from the chlorenchyma cells, sometimes interrupted by sclerenchyma (Fig. 2) or thick walled cells (Fig. 5). The inner, or mestome, sheath is complete or interrupted by sclerenchyma girders, cells relatively large with inner tangential and radial cell wall thickening (Figs. 4 and 7). The cells of the inner sheath adjacent to the xylem are larger; the cells of the inner sheath adjacent to the phloem fibers are smaller and sometimes not distinguishable from the latter. *Adaxial and abaxial sclerenchyma*: adaxial sclerenchyma associated with the vascular bundles occurs as strands or girders. The strands are not in contact with the vascular bundle sheaths. They are separated by mesophyll (chlorenchyma or colorless parenchyma thick walled cells) (Fig. 3). Girders can be in contact with or interrupting the bundle sheath (Fig. 7). Both strands and girders can be present or absent. In permanently infolded leaves, the sclerenchyma may be exhibited as follows: abaxial triangular strands opposite vascular bundles, e.g., *C. eminens* (Fig. 1i); continuous abaxial subepidermal layers, not connected to the vascular bundles by girders, e.g., *C. chrysantha* (Presl) Steud., *C. amoena* (Pilger) Pilger, *C. aurea* (Munro) Hack. (Figs. 1f, 1e, and 1n); continuous, abaxial, subepidermal layers connected to bundles by girders, e.g., *C. ampliflora* (Fig. 1a); continuous, abaxial subepidermal layers connected to bundles by girders, and girders connected to bundles from the adaxial surface, e.g., *C. mollis* Pilger (Fig. 1h). *Sclerenchyma between bundles*: sclerenchyma present or absent between vascular bundles. When present, it occurs as strands of hypodermal layers with girders extending to vascular bundles or not (Figs. 1d, 1e, 1i, 1j, 1l, and 1n). *Sclerenchyma in leaf margin*: present or absent; when present, cape or hood shaped, presenting ranges of size and shape (Figs. 1f and 1h). *Mesophyll*: the chlorenchyma is composed of isodiametric or irregularly shaped cells, sometimes with air spaces. In some species, the chlorenchyma constitutes a relatively small part of the whole unit, arranged in layers following the shape of the ribs and furrows, as in *C. ampliflora* (Figs. 1a and 5) and *C. chaseae* Lucas (Figs. 1l and 2), with the rest of the mesophyll filled with thick walled, colorless parenchyma cells or sclerenchyma. There is no differentiation

between palisade and spongy parenchyma (Fig. 7). Thick walled parenchyma or elongate cells can be present or lacking in the leaf mesophyll. When they are present, the parenchyma cells can be localized over the vascular bundles, forming an arch or continuous girder from the vascular bundle sheath to the adaxial epidermis (Fig. 2). The bulliform cells are restricted to the furrows on the adaxial surface, with a very thin wall. The number of bulliform cells is 5-8, conspicuously large or well defined cells gradually larger than the rest of the epidermal cells (Fig. 4).

The microscopic anatomical examination of species of subsection *Stylagrostis* was made to investigate the similarities and differences that may exist in the general and detailed internal structure of different species in leaf cross section in order to relate leaf structure to ecological characteristics. As was shown by Tuerpe (1962), altitudinal differences determined two types of leaf anatomy, based mainly on vascular bundle position with respect to the epidermis. Anatomy of the leaf blade in some species of subsection *Stylagrostis* agreed with what was found by Tuerpe, but the papillae which are a very important adaptation for some species, such as *Calamagrostis eminens*, *C. ovata*, *C. chrysantha*, etc., were not mentioned. Round silica bodies have been described for the species within subsection *Stylagrostis*. Some species have large silica cells with sinuous edges, located over the top of the ridges. Also, *C. mollis* was the only species found to exhibit long hairs. Leaf anatomy of species of subsection *Stylagrostis* is variable, but typically festucoid as was described by Gould & Shaw (1983), Metcalfe (1960), and Prat (1932).

Scanning electron microscope surveys of leaf anatomy and epidermis have brought to light anatomical details that were not previously discernible by light microscopy. Such surveys have provided valuable information for plant taxonomists. Agrostologists have shown the importance of such studies in classifying living and fossil plants (Albers 1980; Flores, Espinoza, & Kosuka 1977; Hilu 1984; Hilu & Wright 1982; Maeda & Miyake 1973; Palmer & Tucker 1981, 1986; Palmer, Gesbert-Jones, & Hutchinson 1985; Terrell & Wergin 1979, 1981; Thomasson 1978a, 1978b, 1980a, 1980b, 1981, 1984, 1986). Silica accumulates in silica bodies contained in silica cells (Gould & Shaw 1983; Parry & Smithson 1964). Scanning electron microscope studies also show that silica accumulates in other epidermal structures such as prickles (Sakai & Sanford 1984; Terrell & Wergin 1981), bulliform cells (Dayanardan, Kaufman, & Franklin 1983; Parry 1958), and the stomatal apparatus (Sakai & Sanford 1984).

Stomata are usually located at the bases and sides of the furrows on the adaxial epidermis, rarely at the top of the ribs (*Calamagrostis cleefii* Escalona), (Fig. 10) associated or unassociated with papillae (Figs. 23, 24, 25, and 38). The stomata are generally arranged in longitudinal rows separated by files of costal or intercostal cells (Figs. 8, 12, 13, and 41). Usually, there is one interstomatal cell between successive stomata (Figs. 8, 9, 12, 13, and 38). The

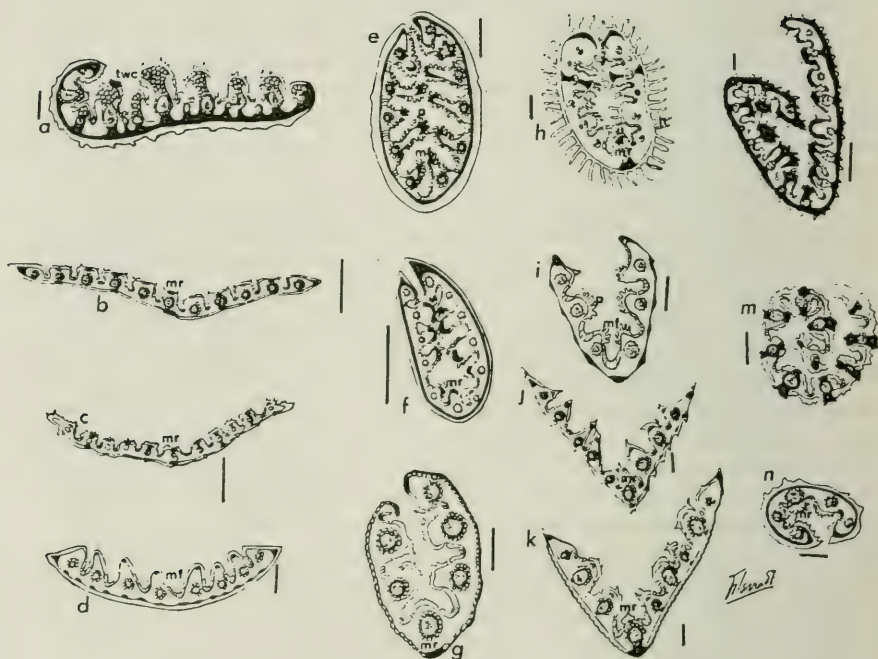
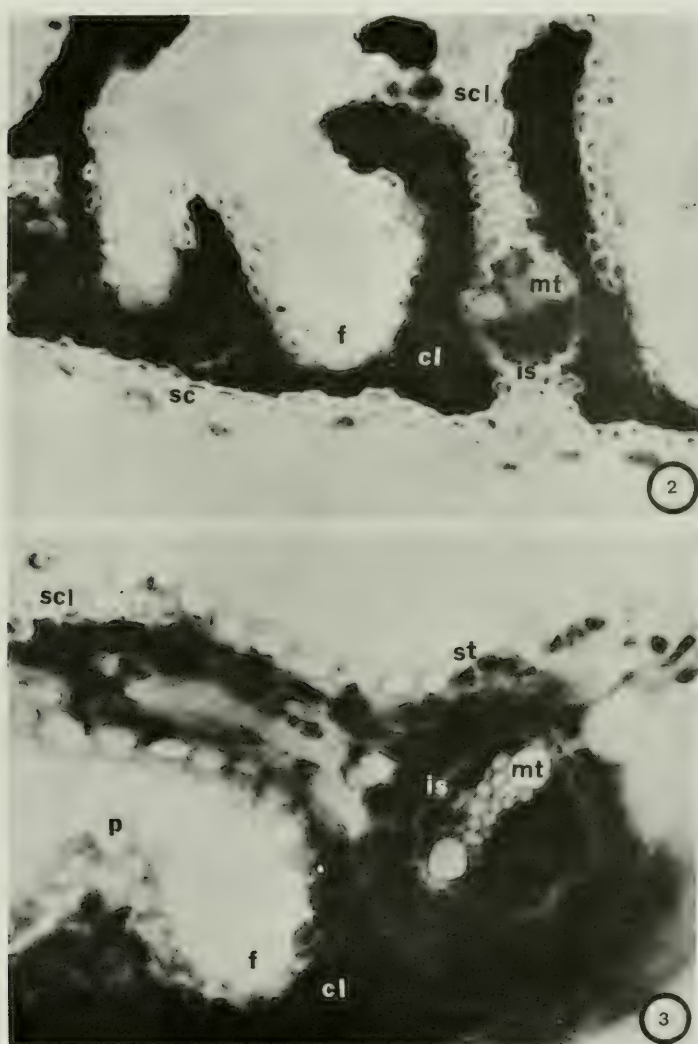
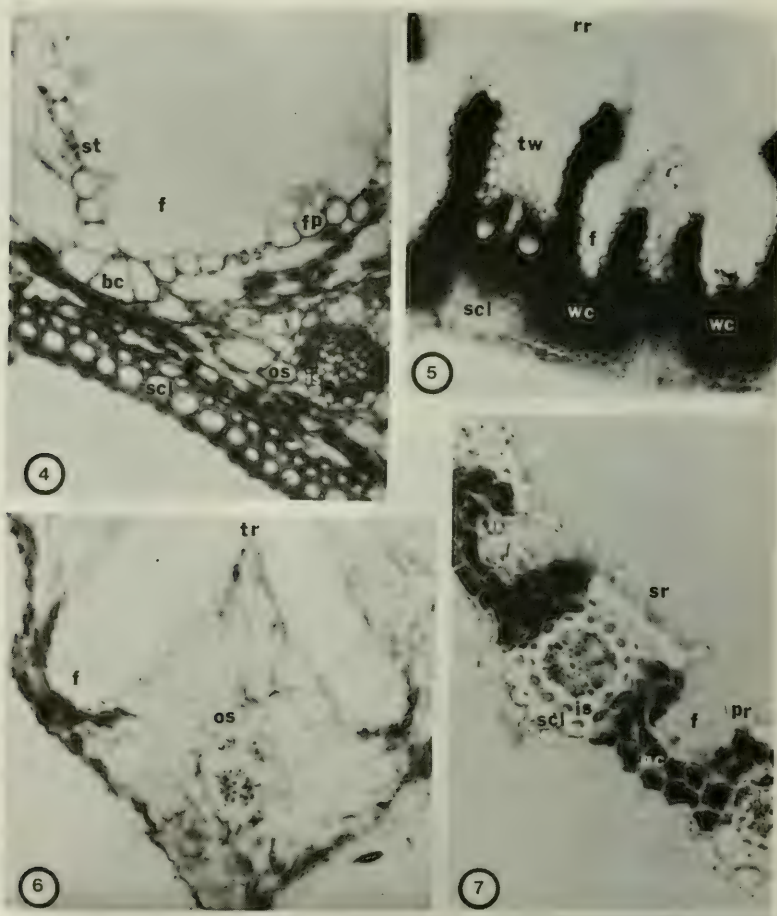


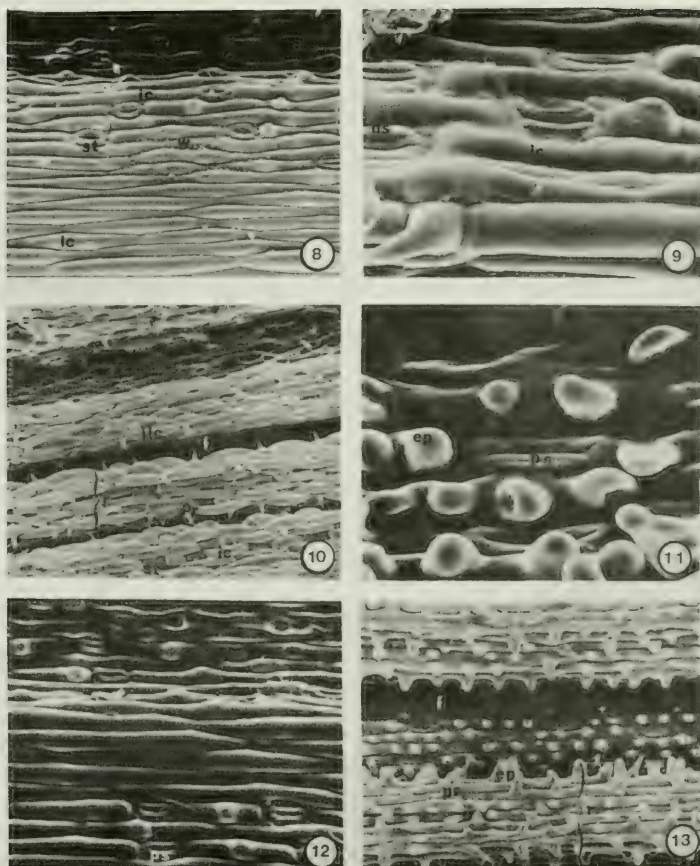
Figure 1. Leaf outline and anatomical structure. Dark areas represent sclerenchyma, white areas represent chlorenchyma, md = midrib, mf = midfurrow, p = papillae, h = long hairs, txc = thick walled parenchyma cells. a) *Calamagrostis ampliflora*, from Hitchcock 22327, bar = 2.5 mm; b) *Calamagrostis guamanensis* Escalona, from Escalona et al. E390, bar = 5.6 mm; c) *Calamagrostis ramonae* Escalona, from Steyermark 55903, bar = 4.3 mm; d) *Calamagrostis ligulata* (H.B.K.) Hitchc., from Ollgaard 10772, bar = 1.3 mm; e) *Calamagrostis chrysantha*, from Escalona et al. B566, bar = 1.0 mm; f) *Calamagrostis aurea*, from Acosta Solia 7223, bar = 4.0 mm; g) *Calamagrostis cleefii*, from Cleef 7768, bar = 1.0 mm; h) *Calamagrostis mollis*, from Asplund 8400, bar = 5.3 mm; i) *Calamagrostis eminens*, from Escalona et al. B669, bar = 1.0 mm; j) *Calamagrostis ovata*, from Turner et al. 1312, bar = 1.0 mm; k) *Calamagrostis curta* (Wedd.) Hitchc., from Solomon et al. 11654, bar = 1.0 mm; l) *Calamagrostis chaseae*, from Lucas 292, bar = 2.0 mm; m) *Calamagrostis pisinna*, from Burandt et al. V0401, bar = 1.0 mm; n) *Calamagrostis amoena*, from Lara et al. 21f, bar = 0.7 mm;



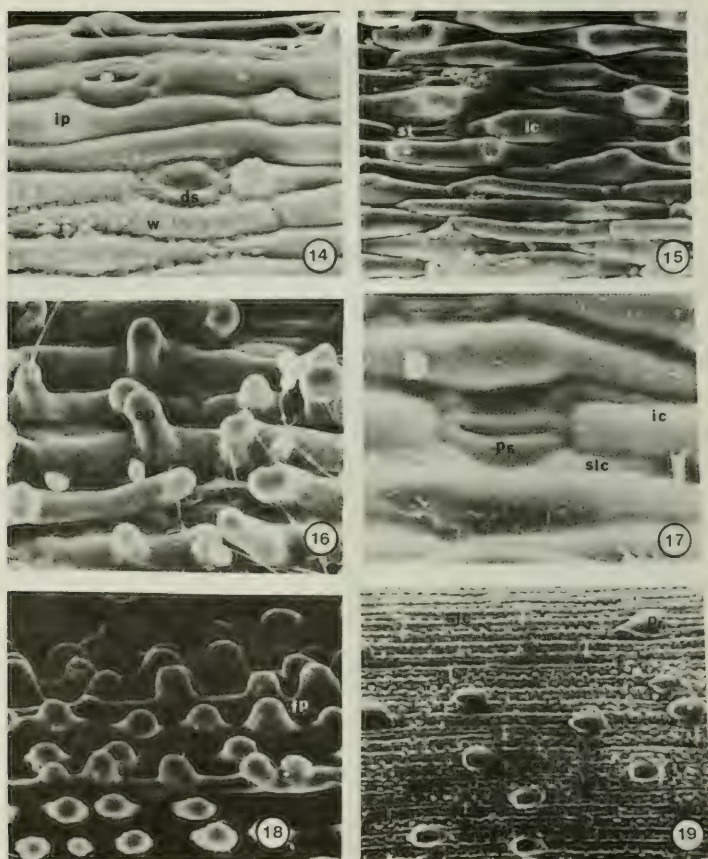
Figures 2 and 3. Leaf blade cross sections from species of subsection *Stylagrostis*. cl = chlorenchyma, f = furrow, is = inner sheath, mt = metaxylem, p = papilla, scl = sclerenchyma. 2) *Calamagrostis chaseae*, from Briceño 229 (X 420). 3) *Calamagrostis chrysantha*, from Escalona et al. B566 (X 560).



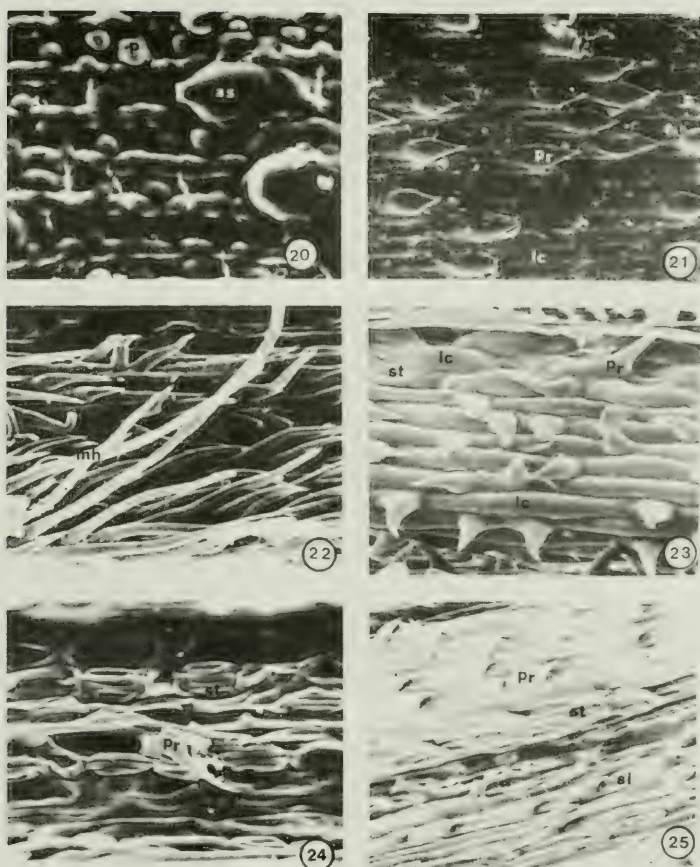
Figures 4-7. Leaf blade cross sections from species of subsection *Stylagrostis*. bc = bulliform cells, cl = chlorenchyma, f = furrow, fp = forked papilla, is = inner sheath, mt = metaxylem, os = outer sheath, p = papilla, pr = prickle, rr = round constricted rib, scl = sclerenchyma, sr = square rib, st = stomata, tr = triangular rib, tw = thick walled parenchyma cells, uc = u shaped chlorenchyma, wc = w shaped chlorenchyma. 4) *Calamagrostis eminens*, from Escalona & D. Smith P420 (X 700). 5) *Calamagrostis ampliflora*, from Hitchcock 22327 (X 480). 6) *Calamagrostis ovata*, from Escalona et al. B547 (X 420). 7) *Calamagrostis pisinna*, from Escalona & Escalona 229 (X 360).



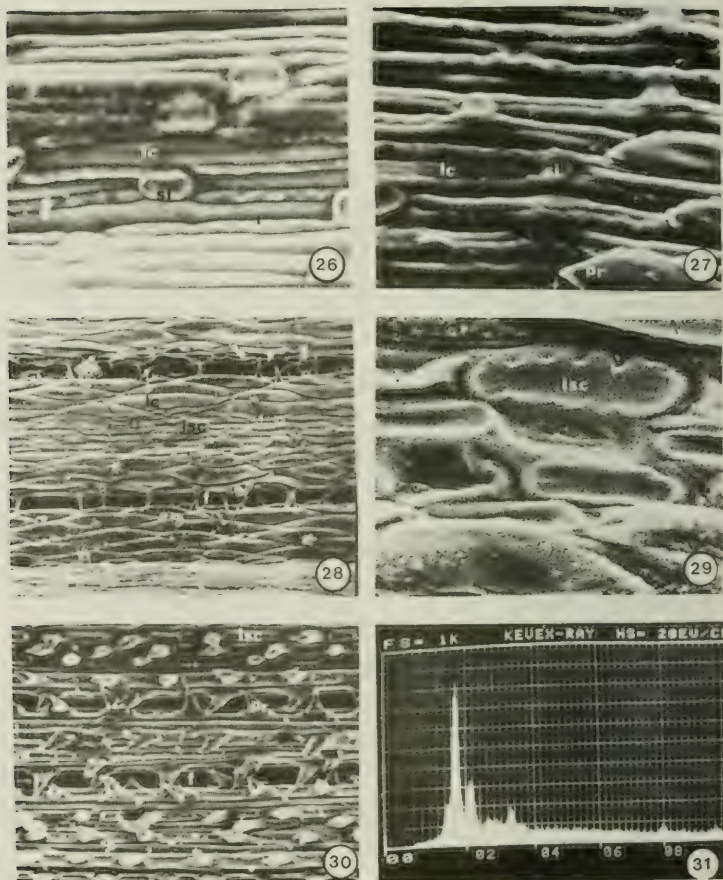
Figures 8-13. Scanning electron micrographs of adaxial epidermis. * = material treated with xylene, # = scanning gamma technique, ds = low dome shaped subsidiary stomata cell, ep = elongated papilla, f = furrow, ic = interstomatal cell, ilc = inflated long cell, pr = prickle, ps = parallel sided subsidiary stomata cell, r = rib, slc = straight edged long cell, st = stomata, w = wax. 8) *Calamagrostis aurea*, from Asplund E7943 (X 260), notice waxy surface #. 9) *Calamagrostis ovata*, from D. Smith & Escalona 19177 (X 720), notice waxy surface. 10) *Calamagrostis cleefii*, from Cleef 7768 (X 160). 11) *Calamagrostis chrysantha*, from Tovar 2530 (X 1100). 12) *Calamagrostis aurea*, from Jameson 95 (X 300) #*. 13) *Calamagrostis eminens*, from Lillo 5045 (X 220).



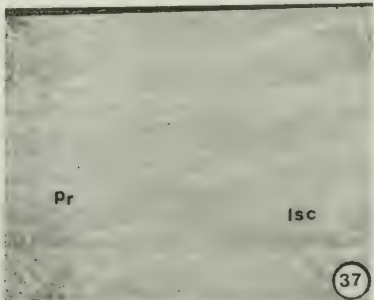
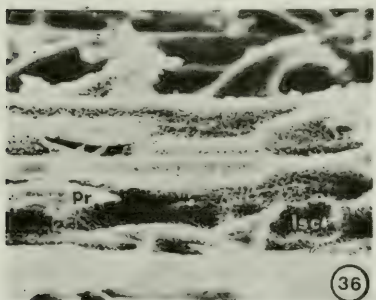
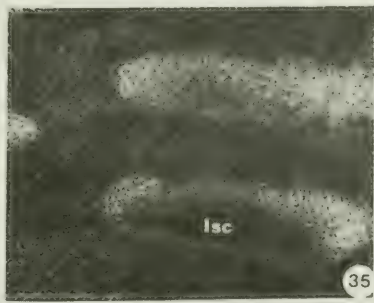
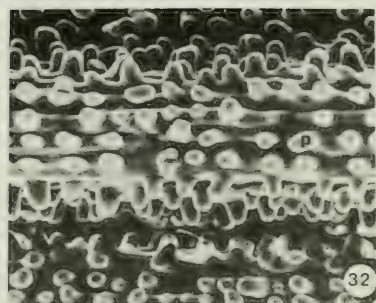
Figures 14-19. Scanning electron micrographs of adaxial or abaxial epidermis. # = scanning gamma technique, dst = low dome shaped subsidiary stomata cell, ep = elongated papilla (4-6 per cell), f = furrow, fp = forked papilla, ic = interstomatal cell, ilc = inflated long cell, ip = inflated papilla, pr = prickle, ps = parallel sided subsidiary stomata cell, slc = sinuous edged long cell. 14) *Calamagrostis aurea*, from Asplund E7943 (X 660) #. 15) *Calamagrostis ovata*, from Escalona et al. B554 (X 440) #. 16) *Calamagrostis chrysantha*, from Escalona et al. B549 (X 940) #. 17) *Calamagrostis ovata*, from Escalona et al. B554 (X 940) #. 18) *Calamagrostis chrysantha*, from Escalona et al. B566 (X 940). 19) *Calamagrostis ovata*, from Escalona et al. B566 (X 240), abaxial epidermis.



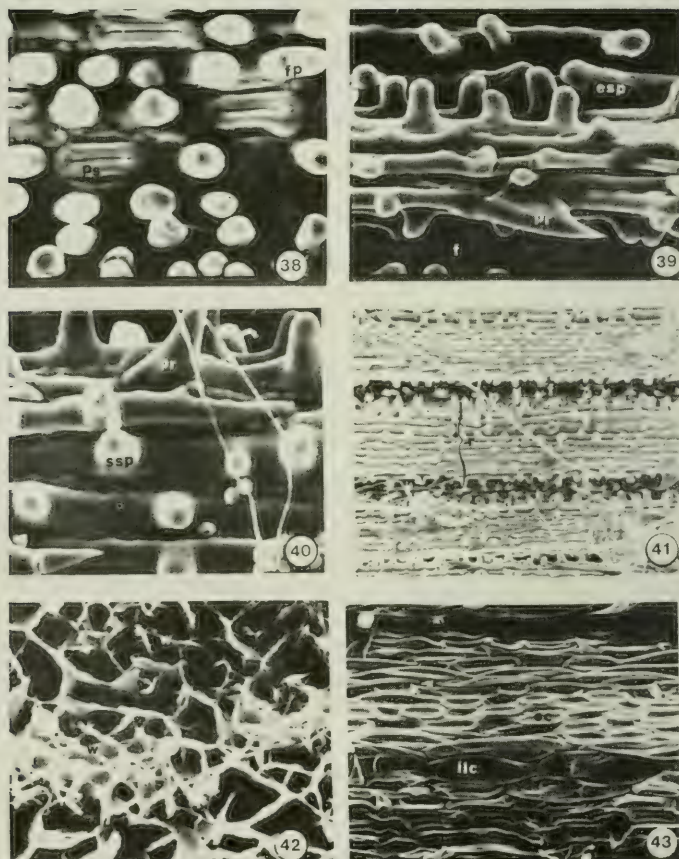
Figures 20-25. Scanning electron micrographs of adaxial or abaxial epidermis. * = material treated with xylene, # = scanning gamma technique, as = asperite, lc = long cell, mh = macrohair, p = papilla, pr = prickle, si = silica cell, st = stomata. 20) *Calamagrostis eminens*, from Solomon 12140 (X 940), abaxial epidermis. 21) *Calamagrostis ampliflora*, from Hitchcock 22327 (X 200), abaxial epidermis. 22) *Calamagrostis mollis*, from Escalona & D. Smith 465 (X 310). 23) *Calamagrostis ampliflora*, from Hitchcock 22327 (X 440). 24) *Calamagrostis curta*, from Solomon et al. 11654 (X 480) *. 25) *Calamagrostis amoena*, from Escalona & Solomon B683 (X 320) #.



Figures 26-31. Scanning electron micrographs of adaxial or abaxial epidermis, and silica spectrum. f = furrow, lc = long cell, lsc = long silica cell with sinuous edges, pr = prickle, si = silica body. 26) *Calamagrostis ligulata*, from Cleef 274 (X 940), abaxial epidermis. 27) *Calamagrostis chrysantha*, from Solomon 4995 (X 300), abaxial epidermis. 28) *Calamagrostis guamanensis*, from Escalona & S. Gallegos E390 (X 60). 29) *Calamagrostis guamanensis*, from Escalona & S. Gallegos E390 (X 60). 30) *Calamagrostis chaseae*, from Briceño 599 (X 240). 31) *Calamagrostis guamanensis*, from Escalona & S. Gallegos E390, showing silica content on long silica cells (adaxial surface).



Figures 32-37. Scanning electron micrographs of adaxial epidermis, with X-ray mapping micrographs for the same areas. lsc = silica cell, p = papilla, pr = prickle, w = wax. 32) *Calamagrostis chrysantha*, from Escalona et al. B549 (X 440). 33) *Calamagrostis chrysantha*, from Escalona et al. B549 (X 440). 34) *Calamagrostis guamanensis*, from Laegaard 53861 (X 1800), wax scales covering surface. 35) *Calamagrostis guamanensis*, from Laegaard 53861 (X 1800). 36) *Calamagrostis chaseae*, from Lucas 292 (X 1000), wax scales covering surface. 37) *Calamagrostis chaseae*, from Lucas 292 (X 1000).



Figures 38-43. Scanning electron micrographs of adaxial epidermis. * = material treated with xylene, # = scanning gamma technique, esp = elongate simple papilla, f = furrow, fp = forked papilla, ilc = inflated long cells with basket type of arrangement, lc = sinuous edged long cell, pr = prickle, ps = parallel sided subsidiary stomata cell, r = rib, sc = silica cell with sinuous edges, ssp = short simple papilla, w = wax. 38) *Calamagrostis chrysantha*, from Vargas 6577 (X 940) #. 39) *Calamagrostis eminens*, from Solomon B669 (X 940) *. 40) *Calamagrostis eminens*, from Lillo 5045 (X 940). 41) *Calamagrostis eminens*, from Escalona & D. Smith P420 (X 200). 42) *Calamagrostis chaseae*, from Lucas 292 (X 6000). 43) *Calamagrostis guamanensis*, from Ollgaard & Balslev 10111 (X 1000) *.

subsidiary cells are parallel sided or slightly low dome shaped. They occur at the same level as epidermal cells or below the level of epidermal cells and are associated or unassociated with papillae (Figs. 4, 9, 11, and 17). *Interstomatal cells*: usually one; long, narrow, sometimes with sinuous edges on the adaxial surface and sometimes bearing one papilla per cell (Figs. 8, 12, 14, and 15) or six papillae (Figs. 11, 13, and 38). *Long cells*: may be flat, slightly dome shaped, with or without sinuous edges, narrowly rectangular, or hexagonal, or with sinuous edges on the adaxial surface, sometimes exhibiting papillae (Figs. 10, 12, 13, 14, 16, 18, 22, 23, 39, 40, 41, and 43) or with sinuous edges on the abaxial surface (Figs. 19, 20, and 21), rarely papillated (Fig. 18). Papillae in long cells of the adaxial surface can be globose (Figs. 9, 14, 15, and 17), elongated or forked (1-6 per cell) (Figs. 11, 13, 16, 18, and 32), and exhibited by some species within subsection *Stylagrostis*, such as *Calamagrostis eminens*, *C. aurea*, *C. chrysantha*, and *C. ovata*. *Prickles*: robust, tough, sharply pointed or rounded end structures with swollen bases and lignified walls making the leaf surface or margins scabrous. The number, distribution, and form vary from one species to another (Figs. 13, 19, 20, 21, 22, 23, 24, 25, and 39). Sometimes prickles accumulate silica as in *C. chaseae* (Figs. 36 and 37). They are present mostly over the ribs or costal zones adaxially or abaxially (Figs. 22, 23, 24, and 25). Prickles can be found on the intercostal zone and usually have globose bases. *Short cells*: found over the veins; solitary or paired but mostly in short rows. *Silica cells*: mostly costal, longitudinally elongate with round ends and sinuous or nodular outlines on the adaxial epidermis (Figs. 25, 28, 29, 30, and 43), rounded to elongate on the abaxial epidermis (Figs. 26 and 27). *Macrohairs*: short or elongated in the adaxial and/or abaxial epidermis of *C. mollis* (Fig. 22). *Epicuticular wax*: scales over the adaxial surface covering the cuticle (Figs. 14, 16, 17, 34, and 36).

Leaf cross sections were observed using light microscopy, but some structures were also examined under the scanning electron microscope. The pictures were taken orienting the long axis of the leaf horizontally, and scanning both abaxial and adaxial epidermis. It was observed that besides the round and dumbbell shaped silica bodies described for the subfamily Pooideae, the accumulation of silica also occurs in subsection *Stylagrostis* in long cells with sinuous edges (Figs. 34 and 35). Silica also was found in prickles (Figs. 36 and 37) and in papillae (Figs. 32 and 33). The presence of silica in silica cells was detected using energy dispersal X-ray analysis to clarify their structure. The amount of silica in silica cells was detected as shown in caption for Figure 31.

Papillae are not characteristic of the Poid type of epidermis (Prat 1932, 1936; Metcalfe 1960), but they occur in subsection *Stylagrostis*. They can be present or absent on all long cells, never overarching the stomata (Figs. 11, 13, and 15) in the adaxial epidermis. The development of papillae seems to be a water retention adaptation to environmental conditions in plants inhabiting paramo and puna in the Andes of South America.

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TRANSFER OF TWO SPECIES OF *SENECIO* TO *PSEUDOGYNOXYS*
(ASTERACEAE-SENECIONEAE)

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ABSTRACT

Senecio boquetensis Standley, from Panamá, and *S. telembina* J. Cuatrecasas, from Colombia, are transferred to the genus *Pseudogynoxys*. Cuatrecasas (1986) recognized the latter as the sole member of his genus *Garcibarrigoa*. *Senecio boquetensis* appears to stand somewhere between *Pseudogynoxys* and *Garcibarrigoa*; indeed, most of the characters which distinguish between the two genera (except habit) would be erased were *S. boquetensis* to be positioned in *Garcibarrigoa*, hence their treatment in *Pseudogynoxys*.

KEY WORDS: *Pseudogynoxys*, *Garcibarrigoa*, *Senecio*, Asteraceae, Senecioneae

Interest in the generic limits of *Pseudogynoxys* for a treatment of the Mexican species, has prompted the present transfers. *Pseudogynoxys* was treated by Greenman (1902) as a subgenus of *Senecio*. Cabrera (1950) elevated the group to generic rank and this has been followed by several recent workers (e.g., Robinson & Cuatrecasas 1977; Nordenstram 1977; Turner, in prep). It is largely distinguished from its closest relatives in *Senecio* (sensu lato, excluding *Gynoxys*) by its acute penicellate stylar appendages, orange or orange yellow rays, and usually vinelike or clambering habit. *Pseudogynoxys* is presumably closely related to *Gynoxys*, and the characters used to distinguish between these two genera are discussed briefly by Robinson & Cuatrecasas (1977) in their synopsis of *Pseudogynoxys*.

Cuatrecasas (1986) erected the monotypic genus *Garcibarrigoa* to accommodate *Senecio telembina*, a species which he thought possibly derived from an early phyletic line leading to *Pseudogynoxys*, but sufficiently different to merit generic rank. He distinguished *Garcibarrigoa* from *Pseudogynoxys* by the following couplet (as translated by Dr. Linda Escobar):

Collar of the anther filament cylindrical. Leaf sheath closed, tubular at base. Leaf blade with proximal veins ascending, parallel, in an acute angle. Pollen sacs rounded at base; endothelial cells with nodules aligned along the lateral walls. Heads radiate. Corollas yellow or orange. Plants herbaceous, creeping at base, hydrophilous. *Garcibarrigoa*

Collar of the anther filament thickened at the base. Leaf sheath always open. Leaf blade with veins separate, spreading. Pollen sacs obtuse or auriculate at base; endothelial cells oblong, with nodules along transverse walls, some (marginal) also with nodules along lateral walls. Heads radiate or discoid. Corollas orange, turning (sometimes) reddish or purple. Robust suffruticose lianas. *Pseudogynoxys*

Senecio boquetensis possesses attributes of both these taxa, having the following characters of *Garcibarrigoa*: leaf blades with ascending parallel veins forming acute angles with the midrib; pollen sacs rounded at base; heads radiate; corolla orange; plants herbaceous. The remaining characters (collar thickened at base, nonclosure of sheath, and endothelial cells) appear to be those of *Pseudogynoxys*.

Even prior to my "discovery" of *Senecio boquetensis* as closely related to *S. telembina*, I had concluded that the combination of characters propounded by Cuatrecasas for the recognition of *Garcibarrigoa* was tenuous at best, and that its submergence in *Pseudogynoxys* was a more reasonable alternative, for the only clear characters separating the two genera are leaf venation and habit. Recognition of *S. boquetensis* within an expanded *Pseudogynoxys* makes better sense to me; so positioned, it must also pull *S. telembina* into that complex. The necessary nomenclature follows:

***Pseudogynoxys boquetensis* (Standl.) B. Turner, *comb. nov.* BASIONYM:**
Senecio boquetensis Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22:394. 1940.

When originally described, Standley noted that "The species appears to be an isolated one, altogether different in appearance from any other known from Central America." This is largely true because of its habit; were it a clambering liana it would readily be positioned near *Pseudogynoxys chenopodioides* (H.B.K.) Cabrera (= *Senecio chenopodioides* H.B.K.), a common species of Central America. Barkley (1975), in his treatment of *Senecio boquetensis* for the *Flora of Panama*, did not comment upon its possible relationship.

***Pseudogynoxys telembina* (J. Cuatrecasas) B. Turner, *comb. nov.* BASIONYM:** *Senecio telembinus* J. Cuatrecasas, Cienca Mex. 24:122. 1965.

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**NESOMIA CHIAPENSIS (ASTERACEAE - EUPATORIEAE), A NEW GENUS
AND SPECIES FROM MÉXICO**

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ABSTRACT

Nesomia chiapensis, a new genus and species from Chiapas, México, is described and illustrated. Because of its conical, paleaceous receptacle, it is believed to be most closely related to the monotypic Peruvian genus *Ferreyella* S.F. Blake (subtribe Ageratinae, sensu King & Robinson).

KEY WORDS: Asteraceae, Eupatorieae, *Nesomia*, México

Routine identification of Mexican Asteraceae has revealed the following novelty.

Nesomia chiapensis B. Turner, *gen. et sp. nov.* Fig. 1. TYPE: MÉXICO. Chiapas: "between Cañada Honda (1300 m) to El Triunfo (2100 m), along southern slopes Sierra de Soconusco to crest . . .", reportedly growing in "moist shaded areas", 6 Nov 1945, *E.H. Xolocotzi & A.J. Sharp X-366* (HOLOTYPE: NY!).

Ferreyellae peruviana S.F. Blake similis sed differt habitu robustiore (usque ad 1.5 m alto), foliis plerumque oppositis, capitulescentia pluricephala congesta ac paniculati-corymbosa, bracteis involucri 2-nervatis, et ramis styli linearibus.

Perennial (?) herbs to 1.5 m high. Stems terete, puberulent to glabrate. Leaves opposite, 10-15 cm long; petioles 3-5 cm long; blades thin, ovate to deltoid, glabrous or nearly so, the primary nerves 3-5, arising from the base, these weakly dichotomously branched above, the margins coarsely serrate. Heads eradiate, arranged in congested, terminal, paniculate corymbs, the ultimate peduncles puberulent, mostly 1-3 mm long. Receptacles conical, paleate, 1.5-2.0 mm high, ca. 0.75 mm wide, the pales well developed and grading into



Fig. 1. *Nesomia chiapensis*, from holotype.

the involucre bracts. Involucres campanulate, 2.5-3.5 mm high, the bracts oblanceolate, subequal, glabrous, ribs 1-2(-3), these well developed, the margins ciliate. Florets perfect, 12-14 per head. Corollas light purple (according to label data), ca. 2 mm long, the tube ca. 0.75 mm long, pubescent with both glandular and nonglandular hairs, the limb ca. 1.25 mm high, the throat broadly flaring, the lobes somewhat irregular, 0.5-0.6 mm long. Anthers ca. 0.6 mm long, the appendages abortive or much reduced, wider than long, the endothecial walls with subquadrate cells having nodular thickenings, the collar linear with more or less ornate cells. Style branches linear, ca. 1.5 mm long. Achenes epappose, 4-5 ribbed, glabrous, ca. 1.5 mm long, having a well defined apical callous upon which the corolla tube sits flush, the carpodium a sharply differentiated callous nubbing.

In King & Robinson (1987) the species will key to the genus *Ferreyella* S.F. Blake, an Andean genus from Perú positioned in their subtribe Ageratinae. *Ferreyella* contains but a single species, *F. peruviana* S.F. Blake (including *F. cuatrecasasii* R.M. King & H. Robinson). *Ferreyella* has receptacular, floral, and fruit characters of *Nesomia*, including conical markedly paleaceous, receptacles. *Nesomia* is readily distinguished, however, by its habit (robust opposite leaved herbs to 1.5 m high with many headed corymbose paniculate cymes; vs. delicate, mostly alternate leaved, annual herbs to 0.3 m high with few headed cynules, nervate involucre bracts, and weakly papillose, linear, stylar appendages).

Among North American genera of the Eupatorieae, *Nesomia chiapensis*, with its chaffy, markedly conical receptacle is an exceptionally distinct taxon. Its habit, capitulescence, and eximbricate involucre resemble those of the genus *Ageratina* (subtribe Oxylobinae), but floret structure, especially the small, nearly exappendiculate anthers (as noted above) suggest that its closest relationship is with *Ferreyella*.

King & Robinson (p. 17) note that the relatively few markedly paleaceous species of the tribe Eupatorieae are "rarely closely related to each other", which is true. They further comment, however, that paleaceous forms "seem to represent an erratic capacity in the Eupatorieae for revival of this suppressed structure." In the case of *Ferreyella* and *Nesomia*, however, I would argue that the strongly conical receptacle with persistent pales that grade into the involucre bracts, is relictual. This view is consistent with the chloroplast DNA restriction site analyses (Kim *et al.* 1989) which place the tribe Eupatorieae as a clearly defined subset that clusters *within* the tribe Heliantheae (*sensu lato*), most members of which possess paleaceous receptacles. In short, receptacular pales in the Eupatorieae appear to have persisted in various phyletic lines of the tribe, these not arising *de nova* as sporadic appendages in an otherwise epaleate tribe as envisioned by King & Robinson, who would position the Eupatorieae as "primitive" or ancestral to the tribe Heliantheae. To quote them directly (p. 15), "the [phyletic] point of departure of the Eupatorieae

is believed to be below the point of divergence of the Heliantheae from the remaining [subfamily] Asteroideae, and close to the point of divergence of the Asteroideae and [subfamily] Cichorioideae."

It is a pleasure to name this remarkably distinct genus for my colleague and peer, Dr. Guy Nesom, Curator of the University of Texas, Austin herbaria (LL, TEX), and unexcelled doyen of the tribe Astereae in North America.

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OVERVIEW AND ANNOTATED LIST OF NORTH AMERICAN SPECIES OF
HEDYOTIS, *HOUSTONIA*, *OLDENLANDIA* (RUBIACEAE), AND
RELATED GENERA

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ABSTRACT

This paper provides a taxonomic overview and an annotated list of 53 species of *Hedyotis*, *Houstonia*, *Oldenlandia*, *Carterella*, *Oldenlandiopsis*, and *Pentodon* (Hedyotideae: Rubiaceae) occurring in the continental United States, Canada, and México. Taxonomic characters and relationships are discussed. *Houstonia* is newly divided into three subgenera. The list gives synonyms, geographic distribution, and comments. Two new combinations are *Houstonia spellenbergii* and *Hedyotis asperuloides* Benth. var. *brandegeana*. Appended is a brief listing of accepted names and summarized distribution.

KEY WORDS: Rubiaceae, Hedyotideae, *Hedyotis*, *Houstonia*, *Oldenlandia*, *Carterella*, *Oldenlandiopsis*, *Pentodon*

This paper presents a taxonomic overview and an annotated list (including synonyms, distribution, and occasional comments) for 53 species of *Hedyotis*, *Houstonia*, *Oldenlandia*, *Carterella*, *Oldenlandiopsis*, and *Pentodon* in the continental United States, Canada, and México (excluding West Indies). A revision of the first three of these genera for this area is in progress, but meanwhile I wish to provide these new data for reference and consideration. Following the annotated list is a short alphabetical listing of accepted names with major synonyms, if any, and summarized distribution.

The classification of *Hedyotis*, *Houstonia*, and *Oldenlandia* (hereafter abbreviated *HHO*) has been controversial for many years. Asa Gray, for example, over a span of 35 years of writing manuals of the North American flora, at first, following Torrey & Gray (1841), accepted *Hedyotis* for the species in the southwestern U.S. (Gray 1849), but in 1853 he dropped *Hedyotis* in favor of *Oldenlandia*. Finally, in the fifth edition of his manual (1867) and in his

Synoptical Flora of North America (1884), he recognized only *Houstonia* and *Oldenlandia*.

Fosberg (1943), Bremekamp (1952), and Rogers (1987) have published reviews of the pertinent literature. Fosberg has recognized only one broad genus, *Hedyotis*, based originally on his studies (1937, 1943) of the Polynesian Rubiaceae. In a 1943 paper he recognized five Polynesian subgenera of *Hedyotis*, but commented that "many botanists would regard these groups as genera." Lewis in earlier papers recognized only *Hedyotis*, but later (1964 and others) upgraded *Oldenlandia* also to generic status. Terrell revised the *Houstonia purpurea* L. group (1959) and later (1975) pointed out the marked differences among the type species of *Hedyotis*, *Houstonia*, and *Oldenlandia*. Verdcourt (1976) in treating East African species of *Oldenlandia* espoused some degree of splitting in stating that "If all the genera closely related to *Hedyotis* are sunk into it, then it forms an unwieldy unit covering a very wide range of structure and habit." Since 1975, in several papers, I have accepted *Houstonia* as including the North American *Hedyotis* species. Terrell, Lewis, Robinson, & Nowicke (1986) furnished data concerning seed types, chromosome numbers, and pollen morphology for 39 North American *Houstonia* species (including *Hedyotis* and excluding *Oldenlandia*), but did not propose a reclassification. In a synopsis of *Oldenlandia* (1990) I stated that I then recognized in North America (excl. West Indies) approximately 20 *Hedyotis* species, 20 *Houstonia*, and ten *Oldenlandia*. This is the taxonomic viewpoint presented here also for 21 species of *Hedyotis*, 20 of *Houstonia*, nine of *Oldenlandia*, and one each for *Pentodon*, *Carterella*, and *Oldenlandiopsis*. For the first time, I have subdivided *Houstonia* into three subgenera, each with different base chromosome numbers and ranges of seed types.

TAXONOMIC CHARACTERS

My present studies emphasize seed characters, based on SEM micrographs of some 60 species of *HHO*. Three additional important kinds of characters that together show the true relationships are chromosome numbers, pollen morphology, and geographic distribution. This is not to say that other characters are not significant, but they are generally less significant and have to be used together with the four main characters. The other significant characters include inflorescence type, corolla shape and size, kind of styly, anther and stigma characters, and capsule shape, size, extent of being inferior, wall thickness, and dehiscence.

The general similarities of many of the species in corolla size and shape, and capsule shape have been an important factor in leading some taxonomists to lump the genera together. The corolla shape and size are often similar in related species, but in other instances may be quite misleading as guides to

relationships. One of the best examples of dissimilar corollas among related species are *Houstonia rubra* Cav. of southwestern U.S. and northern México, and *H. subviscosa* (Wright ex A. Gray) A. Gray and *H. croftiae* Britton & Rusby, both south Texas endemics. The first species has long (9-37 mm), salverform, purplish or pinkish corollas; the latter two species have very short (1.5-3.0 mm), white, tubular-funnelform corollas. If classified on corolla characters alone the species might be placed in separate genera, *H. rubra* being in *Houstonia* or *Hedyotis* because of its large flowers, and *H. subviscosa* and *H. croftiae* in *Oldenlandia*, which often has small, inconspicuous flowers (*H. subviscosa* was originally described in *Oldenlandia*). Consideration of other characters of these species leads, however, to different conclusions. All three species have the same basic chromosome number ($x = 11$), similar seeds, and coporate pollen. They were placed in pollen group 2 by Lewis (1965). All three species are members of the southwestern United States-northern México group of 10 species considered here as *Houstonia* subg. *Ericotis*.

A case of similar corollas in less closely related species is provided by another small south Texas endemic, *Houstonia parviflora* Holzinger ex Greenm. (*Hedyotis greenmanii* Fosb. in Shinners). This has small corollas similar to those of *H. subviscosa* and *H. croftiae*, and thus might be classified with them. Its inflorescence type, however, is cymose and its seeds are unlike those of the other two species, being more like those of the *Houstonia purpurea* group (*Houstonia* subg. *Chamisme*), although with a deeper ventral depression. *Houstonia parviflora* is a somewhat anomalous species, but has the $x = 11$ basic chromosome number, and I have placed it with the other species in *Houstonia* subg. *Ericotis*, but in a separate section. This species illustrates again that corolla shape and size alone may be misleading, and also provides an example of an anomalous species that does not fit clearly into an established species group.

Another example of two unrelated species with similar corolla shapes and sizes are *Houstonia purpurea* of the eastern and central U.S. and *Hedyotis latifolia* (Martens & Galeotti) Walpers (*Houstonia gracilis* Brandegees) of southern México. These look somewhat alike in their small funnelform corollas and in having ovate leaves and the same general habit and size. These two species differ in their chromosome numbers ($x = 6$ in the former, $x = 17$ in the latter) and in their seed morphology (cymbiform with a hilar ridge versus flat with punctiform hilum), and belong to two different phyletic lines.

Another instance of corolla differences is provided by *Houstonia pusilla* Schoepf, the small or southern bluets, and the closely related species *H. micrantha* (Shinners) Terrell. The former species has purplish, salverform corollas similar to the blue ones in *H. caerulea* L., the well known bluets of the eastern U.S., in which the corolla tube is conspicuous. In *H. micrantha* the white corolla is distinctly shorter, and its tube and part of the lobes are covered by the calyx lobes; thus, its corollas differ conspicuously from those of *H. pusilla*,

although at one time *H. micrantha* was treated as a variety of *H. pusilla*. In vegetative characters the two species are so similar that one is hard put to find differences usable in a key. They have similar seeds, the same basic but different actual chromosome numbers ($n = 8$ for *H. pusilla* and $n = 16$ for *H. micrantha*), and I have placed them in the same section and series (not set forth here). They often occur together in nature without intermediates, a situation perhaps due to the difference in ploidy.

Genera in other rubiaceous tribes, such as *Diodia* (tribe Spermacoceae), having fruit with a single large seed per locule, may have funnellform corollas resembling those of *HHO*, thus someone unfamiliar with Rubiaceae might think, on the basis of corolla shape alone, that *Diodia* and *HHO* were closely related.

Both homostyly and heterostyly commonly occur in *HHO*. In distylous heterostyly there are two different kinds of flowers on different plants: thrum with exserted anthers and included stigmas, and pin with the reverse. Homostyly and heterostyly may occur in the same section of a subgenus, as in *Houstonia* subg. *Houstonia* that includes the two closely related species *H. caerulea* (a heterostylous perennial) and *H. pusilla* (a homostylous annual). There seems to be a general tendency for homostyly to occur more often in the annuals. Bremekamp (1952:23) in his monograph of African *Oldenlandia* commented about styly that "species provided with heterostylous flowers ... occur in several genera side by side with species provided with isostylous flowers."

Anther and stigma shapes, sizes, and positions differ among *HHO* species, but those in the same species group often have similar anthers and stigmas. Anthers may be linear, elliptic, or oblong, and sessile or on filaments to ca. 4 mm long. The stigmas have two short elliptic or linear lobes; these may vary in one plant, with the developing stigma sometimes appearing subglobose, as in *Hedyotis nigricans* (Lam.) Fosb., but later becoming elliptic. Various species differ in extent of exsertion of anthers and stigma. In *H. caerulea*, the thrum form has anthers sessile and inserted at the distal end of the corolla tube, sometimes visible, sometimes not, with the stigma included near the midpoint of the tube. In some other species the thrum form may have subsessile anthers clearly exserted at the throat or anthers on filaments 1-4 mm long and farther exserted. The pin form of various species likewise differs in extent of stigma exsertion.

Capsules usually are more or less subglobose and scarcely to somewhat compressed. Dehiscence is loculicidal, but often secondarily septical. A conspicuous departure from this occurs in *Oldenlandiopsis* in which the capsules split apart into four segments. In *H. procumbens* (Walter ex J.F. Gmel.) Standl., the capsules may split and the two halves reflex widely; whether these capsules are formed by cleistogamy is so far unknown. Thickness of capsule walls is often similar in related species, as, e.g., in *Houstonia* subg. *Houstonia* in which the walls are generally thin and fragile, compared to *Houstonia* subg.

Chamisme with walls thicker and more solid. Capsules in *Houstonia* are commonly $\frac{1}{2}$ inferior, with the calyx cup or hypanthium covering about $\frac{1}{2}$ of the capsule. This is a basic, important character (like the number of calyx and corolla lobes), but may vary on one plant from $\frac{1}{4}$ to $\frac{3}{4}$. The most striking example of variation in this character among related species occurs in *Houstonia croftiae*, in which the capsules are $\frac{1}{6}$ to $\frac{1}{4}$ ($-\frac{1}{2}$) inferior, but its closely related cousin, *H. subviscosa*, has $(\frac{1}{2})^{\frac{3}{5}}$ to $\frac{4}{5}$ inferior capsules. *Oldenlandia* and some *Hedyotis* species have mostly or fully inferior capsules.

The pollen data included here are based on Lewis (1965) and Lewis & Nowicke in Terrell *et al.* (1986). In the former publication Lewis sorted part of the North American *Hedyotis* and *Houstonia* species into five groups under *Hedyotis*, according to differences in pollen structure. In the second publication Nowicke emphasized exine characters, while Lewis designated three types of pollen aperture structures based on his classification of pollen types. The colporate type A aperture is the most common in the Rubiaceae and Hedyotideae. It is a generalized type from which more specialized aperture types have evolved. The colporate aperture is frequent in *Houstonia*, but unknown in other Hedyotideae. The third type, colporate type B, is an advanced but simpler condition found only in *Houstonia* subgenus *Houstonia*, the *H. caerulea* group of six species.

Hybridization or its absence provides additional evidence on taxonomic alignments. The phyletic groups outlined here as genera or subgenera are genetically isolated entities in nature, as there are no natural hybrids between them. For example, hybrids between *Houstonia* subg. *Caerulea* and *Houstonia* subg. *Chamisme* or *Hedyotis nigricans*, do not occur, although certain species often are found together in nature. The only hybridization known is within groups, such as *Houstonia* subgenus *Chamisme*, including *H. purpurea* and its relatives.

TAXONOMIC CONSIDERATIONS

Consideration of the most important characters, *i.e.*, seed morphology, chromosome number, pollen morphology, and geographic distribution, shows that there are several phyletic lines (certain of these groups were discussed in Terrell *et al.* 1986). These lines are best known in the case of *Houstonia*, which for the first time here includes three subgenera, each genetically isolated and with a characteristic chromosome number(s), range of seed types, pollen morphology, and geographic range. There is some reason to consider each of these a distinct genus, particularly because of the different characteristic chromosome numbers, or alternatively consider subgenus *Houstonia* a distinct genus and the other two subgenera as one or two separate genera. Instead, I have recognized one genus with three subgenera for the following reasons:

(1) Use of the rank subgenus points out the differences but "allows people to continue to use the old binomial." (Davis & Heywood 1963:106); (2) the subgenera *Houstonia* and *Ericotis* are heterogeneous to the extent that each has one species with seeds more similar to species in another subgenus (*H. rosea* [Raf.] Terrell and *H. parviflora*); and, (3) recent usage has often considered *Hedyotis* an all inclusive genus, and to go to the other extreme seems an action likely to meet with skepticism.

The phyletic lines or phylads must have evolved over a considerable period of time and have undergone stabilization of the basic chromosome number followed by diversification into new species suited to various ecological niches. The phylads are not aneuploid series, but groups of 4-10 species with a single consistent basic chromosome number with or without the development of polyploid races (e.g., Lewis & Terrell 1962). Two good examples of such distinct phylads are *Houstonia* subg. *Ericotis* ($x = 11$) with ten diverse species in the southwestern U.S. and México, and the *Hedyotis mucronata* Benth. group ($x = 13$) with seven diverse species in Baja California and one in Arizona.

SUMMARIES OF THE GENERA AND SUBGENERA

Diagnostic data concerning the genera and subgenera are discussed below, with emphasis on seed characters, chromosomes, pollen, and geographic distribution.

Carterella resembles *Bouvardia* in having an unusually long corolla (3-5 cm) and other flower parts distinctly longer than those of any other *HHO* species; the corolla tube is 5-7 times longer than the lobes, compared to other species with a distinctly lower tube-lobe ratio; seeds strongly laterally compressed, a unique character in these groups; chromosome number $x = 13$, suggesting relationship to the *Hedyotis mucronata* group of Baja California, but considerable divergence in isolation; pollen colporate type A; group 1 of Lewis (1965); distribution: Baja California Sur, México. One species: *Carterella alexanderae* (A. Carter) Terrell (Terrell 1987).

Hedyotis L. is primarily an Asian genus of which the type species, *H. fruticosa* L., is native to southern India and Sri Lanka. Terrell (1975) noted that the capsules of this species are fully inferior with a short cupulate extension of the calyx cup or hypanthium, and differs in this and other characters from the North American species. There are many shrubby species in southern Asia that appear to be related to *Hedyotis fruticosa*. Their seeds are generally depressed-conic or more flattened and with a large hilar peak, thus are noncrateriform seeds differing strongly from crateriform seeds. Unfortunately, chromosome and pollen data are few for the Asian species. The *Hedyotis* species in the Hawaiian Islands, Polynesia, and Malaysia are diverse, and generally seem to be only distantly related to the North American species of so called *Hedyotis*.

The foregoing assumes the type to be *Hedyotis fruticosa*. Recently, Rogers (1987) claimed that *H. auricularia* L. is the correct type, although *H. fruticosa* was accepted in the *Index Nominum Genericorum* (Farr et al. 1979). At present, we have to consider this matter as unsettled. An unfortunate consequence of reverting to *H. auricularia* as the type would be that this species has oldenlandioid seeds (and indehiscent capsules) and perhaps is closest to *Oldenlandia*. Any reasonable degree of splitting would consider that the Asian species now in *Hedyotis* would not be sufficiently closely related to *H. auricularia* to be congeneric with it. In this reasonable case, all of the Asian species allied to *H. fruticosa* and presumably all of the North American species now called *Hedyotis* would require new combinations under a new genus name. Consequently, retaining *H. fruticosa* as a conserved type would contribute to nomenclatural stability.

North American *Hedyotis*, as delimited here, includes 21 diverse noncrateriform seeded species (except *Hedyotis vegrandis* W.H. Lewis with unique seeds) from México and the southwestern U.S. They are distinct from *Houstonia* and *Oldenlandia* in seed types, and also have four different chromosome numbers ($x = 9, 10, 13, 17$), but chromosomal data are lacking for some of these species. None of the North American species (possibly excepting *Hedyotis sharpii* [Terrell] Nesom) have seed types similar to seeds of *Hedyotis fruticosa* or to other Asian species of *Hedyotis*. Pollen data for the North American species are incomplete, but, so far as known, include only the aperture types colporate and colpate type B. As applied to North American species, *Hedyotis* is a genus name of convenience for a heterogeneous group, a "dustbin genus" (Davis & Heywood 1963). I am tentatively retaining these under *Hedyotis* pending further study.

Houstonia, restricted to North America, includes 20 species that have crateriform (*sens. lat.*) seeds (except for *Hedyotis vegrandis* with crateriform but otherwise unique seeds; *Hedyotis teretifolia* [Terrell] Nesom seeds have a concave face with a small ridge). The term crateriform has been defined (*e.g.*, Stearn 1966) as more or less cup shaped. I am using it here in two senses: (1) *sens. str.*, meaning cup shaped; (2) *sens. lat.*, meaning with any kind of ventral depression or cavity, including cup shaped, saucer shaped (acetabuliform), boat shaped (cymbiform), or with a subglobose cavity with a ventral orifice, as in the seeds of *Houstonia caerulea*. This genus also has a unique set of chromosome numbers: $x = 6, 7, 8, 11$, although 11 occurs in *Oldenlandiopsis* and in *Oldenlandia microtheca* (Schlecht. & Cham.) DC. of México, neither one closely related to *Houstonia*.

Houstonia includes three newly recognized subgenera: (1) subg. *Houstonia*, the *H. caerulea* group; (2) subg. *Chamisme*, the *H. purpurea* group; (3) subg. *Ericotis*, the *H. rubra* group. The main characters of these subgenera are summarized below.

1. *Houstonia* subg. *Houstonia*.

Seeds subglobose; ventral face with a small orifice opening into a subglobose cavity; hilar ridge lacking; testa reticulate. Chromosome numbers: $x = 8$ for four species, $x = 7$ for two species. Pollen type colporate B; group 5. Distribution: eastern and central U.S. and eastern Canada. Plants mostly vernal flowering. Stems soft, delicate. Leaves small (2-30 mm long), elliptic or ovate or spatulate, uninerved. Flowers heterostylous or homostylous, solitary on long pedicels. Corollas salverform/shortly salverform. Capsules often slightly broader than long, thin walled. Six species; type: *Houstonia caerulea* L. *Houstonia rosea*, like *H. procumbens* in having $n = 7$, differs mainly in its cymbiform seeds with a hilar ridge in a rounded depression; also its corolla tube is flared distally, and its chromosomes are small and uniquely 4-aperturate (Lewis 1965). There were further comments on this species in Terrell 1986a.

This subgenus, as exemplified by *Houstonia caerulea*, is so clearly and amply distinct from *Hedyotis* and *Oldenlandia* that its inclusion in an all embracing *Hedyotis* is clearly wrong. Put another way, even those botanists who would still insist on putting all of these varied groups together in one genus would surely segregate the *Houstonia caerulea* group as all or part of a distinct genus, as it is the one most different from the other taxa. Lewis (1962) rated the *H. caerulea* group as the one evolutionarily most advanced.

2. *Houstonia* subg. *Chamisme* Raf.

Seeds cymbiform or somewhat acetabuliform, moderately compressed dorsiventrally; ventral face with a linear or oblong hilar ridge centered in a shallow oblong or elliptic depression; margin entire, upturned, rimmed, and about as high as the hilar ridge, testa reticulate. Chromosome number $x = 6$. Pollen type colporate; group 4. Distribution: Eastern and central U.S. and southern Canada. Plants (vernal) aestival flowering. Stems fibrous. Leaves medium sized (5-63 mm long), linear to broadly ovate, 1-7 nerved. Flowers heterostylous, cymose. Corollas funnelform. Capsules subglobose, medium-thick walled. The species are basically similar to each other in important characters and form a homogeneous group of species each with its own characteristic geographic range. Four species; type: *Houstonia purpurea* L.

3. *Houstonia* subg. *Ericotis* Terrell, subg. nov. Type: *Houstonia rubra* Cav.

A *Houstonia* subg. *Houstonia* et *H.* subg. *Chamisme* seminibus crateriformibus vel cymbiformibus vel acetabuliformibus, plus minusve compressis dorsiventraliter, crista hilari lineari, in superficie ventrali in depressione vadosa vel profunda, margine integre vel undulata vel lobata, facienti canthum erectum, curtum vel altum,

sinu vadoso bilobato adnato cristae hilaris extremo in speciebus aliquot, testa reticulata vel areolarum parietibus connatis et foveis complexis vel favosa, interdum torulosa vel projecturis, chromosomatum numero 11 absimilis.

Seeds crateriform *sens. str.*, cymbiform, or acetabuliform, with slight to moderate dorsiventral compression; ventral face with a linear or oblong hilar ridge centric or acentric in a shallow to deep depression; margin entire, undulate, or lobed, forming a low to high upturned rim; margin in some species with a small bilobed sinus fused with one end of the hilar ridge; testa reticulate or the areole walls coalesced and complexly pitted or honeycombed, sometimes with surface knobs or projections. Chromosome number $x = 11$. Pollen type colpororate; group 2. Distribution: Mainly southwestern U.S. and/or México. Plants vernal or aestival flowering. Stems fibrous or delicate. Leaves medium sized, acerose or linear to elliptic or oblanceolate. Flowers heterostylous or homostylous, cymose or solitary. Corollas funnelform or salverform. Capsules usually subglobose, thick or thin walled. Ten species.

A.P. de Candolle (*Prodromus*, 1830) first used the name *Ereicotis* to refer to a section of *Anotis*, including primarily nine species of the South American genus *Arcytophyllum* and additionally *Anotis cervantesii* (H.B.K.) DC. (*Houstonia wrightii* A. Gray), related to *Houstonia acerosa* (A. Gray) Benth. & Hook. Later, Gray used the section name *Ereicotis* to include *Houstonia acerosa* and *Houstonia fasciculata* A. Gray (*Hedyotis intricata* Fosc.), neither of which are related closely to *Arcytophyllum*. I take up a new name here as a variant spelling in a somewhat different sense for a subgenus, as the section name *Ereicotis* of *Anotis* applied mainly to *Arcytophyllum*. Mena V. (1990) listed *Anotis* section "Ereico[c]tis" and the genus name *Ereicoctis* (DC.) Kuntze as synonyms of *Arcytophyllum*. I agree with this; however, I interpret *Ereicoctis* as Kuntze's misspelling of De Candolle's *Anotis* section *Ereicotis*.

Oldenlandia L., a worldwide genus of herbs in warm, tropical, and subtropical regions, was estimated by Verdcourt (1976) to have about 100 species, of which 61 are in Africa (Bremekamp 1952). Recent African floras have recognized twelve species in West Tropical Africa (Hepper & Keay 1963), seven species in Gabon (Hallé 1966), and 37 species in Tropical East Africa (Verdcourt 1976). These authors did not recognize the occurrence of *Hedyotis* in their regions, and Hallé stated that *Hedyotis* is Asian. As recognized here, *Oldenlandia* has the following principal characteristics: Small annual or perennial herbs; corollas small (usually less than 8 mm long), rotate to funnelform or salverform; homostylous or heterostylous; capsules more or less subglobose, $\frac{4}{5}$ to fully inferior; seeds minute (typically 0.1-0.4 mm long), numerous (usually 50-150 per capsule), trigonous, conic, or tetragonous, hilum punctiform at apex of an angle, testa minutely reticulate, areole walls straight or sinuous; and chromosome number typically $x = 9$ known for many species. The seed

characters and chromosome number especially distinguish *Oldenlandia* from *Hedyotis* and *Houstonia*. Additional comments regarding *Oldenlandia* were included in Terrell (1990) and Terrell & Lewis (1990). Nine species; type: *O. corymbosa* L.

Oldenlandiopsis, a recently described genus (Terrell & Lewis 1990), has narrowly turbinate or obconic capsules (rather than subglobose) that later separate into four narrow segments; chromosome number $n = 11$; pollen is eight aperturate, a unique character also found in *Neanotis*, an unrelated Asian genus; seeds are compressed-subglobose and 20-35 per capsule. One species; *O. callitrichoides* (Griseb.) Terrell & W.H. Lewis.

Pentodon Hochst. is a genus of two African species (Verdcourt 1976; Rogers 1987). *Pentodon pentandrus* (Schumach. & Thonn.) Vatke has stems succulent, brittle; corollas 5 lobed instead of 4; capsules broadly oblong or turbinate (not subglobose); seeds similar to those of *Oldenlandia*, but with numerous tubercles on or near the areole walls; chromosomes with $x = 9$, like *Oldenlandia*. This species is adventive in the southeastern U.S.

DIAGNOSTIC KEYS, BASED PRIMARILY ON SEED CHARACTERS.

The two keys for taxa with crateriform and noncrateriform seeds, respectively, point out some main differences in the seeds of the genera, subgenera, and species groups. Base chromosome numbers are indicated when known, and other data are added when needed. For the *Houstonia* subgenera, the entries are short, as complete data are given in the summaries in the text. Species numbers are those given to the species in the annotated list. Many of these taxa were included in Table 2 of Terrell *et al.* (1986).

KEY 1. Seeds crateriform *sens. lat.*, with a ventral subglobose cavity or a hilar ridge in a ventral depression or concavity.

1. Seed testa with numerous minute pores in each areole (cell); rare Mexican species. *Hedyotis vegrandis*

- 1' Seed testa without pores. (2)

2. Seeds merely concave, with low short hilar ridge fused at one end with the unrimmed margin; rare Mexican species. .. *Hedyotis teretifolia*

- 2' Seeds with cavity or distinct depression. (3)

3. Seeds subglobose, with ventral subglobose cavity, lacking a hilar ridge (*Houstonia rosea* seeds with hilar ridge in depression); $x = 8, 7$; see subgenus summary in text for additional characters.
 *Houstonia* subg. *Houstonia*

- 3' Seeds slightly to moderately compressed, with hilar ridge in a distinct boat shaped to cup shaped depression.(4)
4. Seeds usually boat shaped; hilar ridge in shallow depression; margin entire, rimmed; testa reticulate; $x = 6$; additional characters listed in subgenus summary. *Houstonia* subg. *Chamisme*
- 4' Seeds cup, saucer, or boat shaped, with hilar ridge in shallow to deep depression; margin entire, lobed, or with small bilobed sinus; hilar ridge sometimes fused with margin at one end; testa reticulate or complexly honeycombed with areole walls coalescent; $x = 11$; additional characters listed in subgenus summary.
 *Houstonia* subg. *Ericotis*

KEY 2. Seeds noncrateriform, lacking a ventral cavity or depression; hilum punctiform. (This key includes *Hedyotis*, as noted above, in need of further study; therefore, it deals rather desultorily with some species groups.)

1. Seeds trigonous, conic, or tetragonous; 0.1-0.4(-0.6) mm long; seeds numerous (more than 50) per capsule; $x = 9$. (*Hedyotis sharpii*, an anomalous Mexican species, has seeds somewhat 3 angled, 0.6-0.8 mm long, fewer per capsule).(2)
- 1' Seeds not trigonous, conic, or tetragonous; usually 0.4 or more mm long; fewer than 50 per capsule; chromosome number various.(3)
2. Seeds with testa smooth; floral parts in 4's.
 *Oldenlandia* species 1,2,4,8,9 (and others worldwide)
- 2' Seeds with tubercles on areole walls; floral parts in 5's. .. *Pentodon*
3. Seeds flat or laterally strongly compressed.(4)
- 3' Seeds not as above.(5)
4. Seeds dorsiventrally flat, winged or not; hilum on ventral face; $x = 17$ in *Hedyotis latifolia*; México. *Hedyotis* species 6,7,11,21
- 4' Seeds laterally strongly compressed; hilum on apex of an angle; $x = 13$; México. *Carterella*
5. Seeds irregularly angulate; testa pitted; $x = 11, 12$; México.
 *Oldenlandia* species 3,5,6
- 5' Seeds not conspicuously angulate; testa reticulate.(6)

6. Seeds ellipsoid or ovoid; 0.3-1.7 mm long. (a) *Hedyotis nigricans* and species 1,5,13,19; $x = 9, 10$, or ?; (b) *H. mucronata* and species 2,3,4,7,8,15,16; $x = 13$; (c) *H. intricata*: $x = ?$
- 6' Seeds primarily depressed-subglobose; 0.25-0.50 mm long.
 (a) *Oldenlandia pringlei*: $x = ?$; (b) *Oldenlandiopsis*: $x = 11$

ANNOTATED LIST OF SPECIES

The following alphabetically arranged summary of the genera and species provides accepted names, synonymy, distribution, and comments. The synonymy is complete, except as noted for certain species, such as *Houstonia caerulea* and *Hedyotis nigricans* that have many synonyms. Two new combinations are included: *Houstonia spellenbergii* and *Hedyotis asperuloides* var. *brandegeana*. Data on types are not included in this short summary, although I have these data for most of the species.

Carterella Terrell, *Brittonia* 39:250. 1987.

Carterella alexanderae (A. Carter) Terrell, *Brittonia* 39:250. 1987. BASIONYM: *Bouvardia alexanderae* A. Carter, *Madroño* 13:142, fig. 2. 1955. *Hedyotis alexanderae* (A. Carter) W.H. Lewis, *Ann. Missouri Bot. Gard.* 55:31. 1968.

Distribution: México: Baja California Sur.

Hedyotis L., *Sp. Pl.* 1:105. 1753.

1. *Hedyotis angulata* Fosb. in Shinnery, *Field & Lab.* 17:166. 1949. *Hedyotis nigricans* (Lam.) Fosb. var. *angulata* (Fosb.) W.H. Lewis, *Amer. J. Bot.* 49:865. 1962.

Hedyotis stenophylla Torr. & Gray var. *parviflora* A. Gray, *Pl. Wright.* 1:81. 1852. Non *Hedyotis parviflora* Walp., *Ann. Bot. Syst.* 2:772. 1852, nec *Houstonia parviflora* Holzinger ex Greenm., *Proc. Amer. Acad. Arts* 32:284. 1897. *Hedyotis nigricans* (Lam.) Fosb. var. *parviflora* (A. Gray) W.H. Lewis, *Ann. Missouri Bot. Gard.* 55:32. 1968.

Houstonia rupicola Greenm., *Proc. Amer. Acad. Arts* 32:286. 1897, non *Hedyotis rupicola* Sond. ex Harv. & Sond., *Fl. Cap.* 3:12. 1865.

Distribution: U.S.: Southwestern Texas; México: Coahuila, Chihuahua.

2. *Hedyotis arenaria* (Rose) W.H. Lewis, *Rhodora* 63:221. 1961. BASIONYM: *Houstonia arenaria* Rose in Vasey, G. & J.N. Rose, *Contr. U.S. Natl. Herb.* 1:70. 1890.

Distribution: México: Baja California.

3. *Hedyotis asperuloides* Benth., *Bot. Voy. Sulph.* 19, t. 13. 1844. *Houstonia asperuloides* (Benth.) A. Gray, *Proc. Amer. Acad.* 5:158. 1861.

3a. *Hedyotis asperuloides* Benth. var. *asperuloides*

Distribution: México: Baja California.

- 3b. *Hedyotis asperuloides* Benth. var. *brandegeana* (Rose) Terrell, *comb. nov.* BASIONYM: *Houstonia brandegeana* Rose in Vasey, G. & J.N. Rose, *Contr. U.S. Natl. Herb.* 1:70. 1890. *Hedyotis asperuloides* Benth. f. *brandegeana* (Rose) W.H. Lewis, *Rhodora* 63:221. 1961. *Houstonia asperuloides* (Benth.) A. Gray var. *brandegeana* (Rose) Wiggins, *Veg. & Fl. Sonoran Desert* 2:1400. 1964.

Distribution: México: Baja California.

4. *Hedyotis brevipes* (Rose) W.H. Lewis, *Rhodora* 63:221. 1961. BASIONYM: *Houstonia brevipes* Rose in Vasey, G. & J.N. Rose, *Contr. U.S. Natl. Herb.* 1:83. 1890.

Distribution: México: Baja California.

5. *Hedyotis butterwickiae* (Terrell) Nesom, *Syst. Bot.* 13:434. 1988. BASIONYM: *Houstonia butterwickiae* Terrell, *Brittonia* 31:164. 1979.

Distribution: U.S.: Brewster Co., Texas.

6. *Hedyotis galeottii* (Martens) Terrell & Lorence, *Phytologia* 66:1. 1989. BASIONYM: *Declieuxia galeottii* Martens in Martens & Galeottii, *Bull. Acad. Roy. Sci. Bruxelles* 11:231. 1844.

Manettia liebmannii Standl., *J. Washington Acad. Sci.* 17:337. 1927.

Distribution: México: Veracruz, Oaxaca.

7. *Hedyotis gracilentia* (I.M. Johnston) W.H. Lewis, *Rhodora* 63:222. 1961. BASIONYM: *Houstonia gracilentia* I.M. Johnston, *Proc. California Acad. Sci.*, ser. 4, 12:1174. 1924.

Distribution: México: Baja California.

8. *Hedyotis greenei* (A. Gray) W.H. Lewis, *Rhodora* 63:222. 1961. BASIONYM: *Oldenlandia greenei* A. Gray, *Proc. Amer. Acad. Arts* 19:77. 1883. *Houstonia greenei* (A. Gray) Terrell, *Phytologia* 59:79. 1985.

Distribution: U.S.: Arizona.

9. *Hedyotis intricata* Fosb., *Lloydia* 4:290. 1941.
Houstonia fasciculata A. Gray, *Proc. Amer. Acad. Arts* 17:203. 1882, non *Hedyotis fasciculata* Bertoloni 1850.

Distribution: Southwestern U.S., northern México.

10. *Hedyotis kingii* (Terrell) Nesom, *Syst. Bot.* 13:434. 1988. BASIONYM: *Houstonia kingii* Terrell, *Brittonia* 32:491. 1980.

Distribution: México: Oaxaca.

11. *Hedyotis latifolia* (Martens & Galeotti) Walpers, *Rep.* 6:55. 1846. BASIONYM: *Oldenlandia latifolia* Martens & Galeotti, *Bull. Acad. Roy. Sci. Bruxelles* 11, pt. 1:235. 1844, non *Houstonia latifolia* Willd. ex Roem. & Schult. 1818. The type of *O. latifolia* has flat seeds, providing positive identification that it belongs here. Standley, 1918, erroneously listed it as a synonym of the superficially similar *O. microtheca*, which has angular seeds. The name *H. latifolia* replaces the previously accepted names *Hedyotis erigula* W.H. Lewis and *Houstonia gracilis*.

Hedyotis dichotoma Sessé & Moçino, *Fl. Mexic.*, ed. 1. 22. 1893, non *Hedyotis dichotoma* Cav. 1801.

Houstonia gracilis Brandege, *Zoe* 5:238. 1907, non *Hedyotis gracilis* DC., *Prodr.* 4:419. 1830.

Hedyotis erigula W.H. Lewis, *Rhodora* 63:221. 1961.

Distribution: México: Veracruz, Chiapas, Oaxaca; Guatemala.

12. *Hedyotis mucronata* Benth., *Bot. Voy. Sulph.* 19. 1844. *Houstonia mucronata* (Benth.) B.L. Robinson, *Proc. Amer. Acad. Arts* 45:401. 1910.

Houstonia fruticosa Rose, *Contr. U.S. Natl. Herb.* 1:132. 1892.

Distribution: México: Baja California.

13. *Hedyotis mullerae* Fosb., Lloydia 4:288. 1941. *Houstonia mullerae* (Fosb.) Terrell, Brittonia 31:169. 1979.

Distribution: México: Coahuila.

14. *Hedyotis nigricans* (Lam.) Fosb., Lloydia 4:287. 1941.

14a. *Hedyotis nigricans* (Lam.) Fosb. var. *nigricans* BASIONYM: *Gentiana nigricans* Lam., *Encycl.* 2:645. 1788. *Houstonia nigricans* (Lam.) Fern., Rhodora 42:299. 1940.

Partial synonymy follows; some additional synonymy given by Terrell (1986), under *Houstonia*.

Houstonia angustifolia Michx., *Fl. Bor. Amer.* 1:85. 1803.

Hedyotis stenophylla Torr. & Gray, *Fl. N. Amer.* 2:41. 1841.

Houstonia salina A.A. Heller, Contr. Herb. Franklin and Marshall Coll. 1:96, pl. 9. 1895.

Houstonia tenuis Small, *Fl. S.E. U.S.* 1109, 1338. 1903.

Distribution: Southeastern U.S. through Florida; Michigan and Ohio west to Arizona, eastern Colorado, Nebraska, and Iowa; México: North and central.

Comment: *Hedyotis nigricans* is a polymorphic species.

- 14b. *Hedyotis nigricans* (Lam.) Fosb. var. *floridana* (Standley) Wunderlin, Sida 11:400. 1986. BASIONYM: *Houstonia floridana* Standl., *N. Amer. Fl.* 32(1):36. 1918. *Hedyotis purpurea* (L.) Torr. & Gray var. *floridana* (Standl.) Fosb., Castanea 19:36. 1954. *Houstonia nigricans* (Lam.) Fern. var. *floridana* (Standl.) Terrell, Phytologia 59:79. 1985.

Distribution: U.S.: Dade and Monroe counties, Florida; Bahamas.

Comment: Discussed by Terrell (1986b).

- 14c. *Hedyotis nigricans* (Lam.) Fosb. var. *pulvinata* (Small) Fosb., Castanea 19:37. 1954. BASIONYM: *Houstonia pulvinata* Small, Bull. New York Bot. Gard. 1:289. 1899. *Houstonia nigricans* (Lam.) Fern. var. *pulvinata* (Small) Terrell, Phytologia 59:79. 1985.

Distribution: U.S.: St. Johns and Flagler counties, Florida.

Comment: Discussed by Terrell (1986b).

15. *Hedyotis peninsularis* (Brandeggee) W.H. Lewis, Rhodora 63:222. 1961. BASIONYM: *Houstonia peninsularis* Brandeggee, Zoe 5:160. 1903.

Distribution: México: Baja California.

16. *Hedyotis saxatilis* W.H. Lewis, *Rhodora* 63:222. 1961.

Houstonia australis I.M. Johnston, Univ. Calif. Pub. Bot. 7:446. 1922, non *Hedyotis australis* W.H. Lewis & D.M. Moore, Southw. Naturalist 3:208. 1959.

Distribution: México: Baja California.

17. *Hedyotis sharpii* (Terrell) Nesom, Syst. Bot. 13:434. 1988. BASIONYM: *Houstonia sharpii* Terrell, Brittonia 32:490. 1980.

Distribution: México: Veracruz, Hidalgo.

18. *Hedyotis teretifolia* (Terrell) Nesom, Syst. Bot. 13:434. 1988. BASIONYM: *Houstonia teretifolia* Terrell, Brittonia 31:166. 1979.

Distribution: México: Coahuila.

19. *Hedyotis umbratilis* (B.L. Robinson) W.H. Lewis, *Rhodora* 63:222. 1961. BASIONYM: *Houstonia umbratilis* B.L. Robinson, Proc. Amer. Acad. Arts 45:401. 1910.

Distribution: México: Coahuila, Nuevo León, Veracruz.

20. *Hedyotis vegrandis* W.H. Lewis, *Rhodora* 63:222. 1961.

Houstonia prostrata Brandegees, Zoe 5:105. 1901, non *Hedyotis prostrata* Korthals 1851.

Houstonia parvula Brandegees, Zoe 5:221. 1905, non *Hedyotis parvula* (A. Gray) Fosb. 1943. *Houstonia prostrata* Brandegees var. *parvula* (Brandegee) Wiggins, Veg. & Fl. Sonoran Desert 2:1399. 1964. *Hedyotis sinaloae* W.H. Lewis, *Rhodora* 63:222. 1961.

Distribution: México: Baja California, Sinaloa, Sonora.

Comment: Var. *parvula* characters strongly overlap with characters of the typical variety.

21. *Hedyotis xestosperma* (Robinson & Greenm.) W.H. Lewis, *Rhodora* 63:222. 1961. BASIONYM: *Oldenlandia xestosperma* Robinson & Greenm., Proc. Amer. Acad. Arts 32:41. 1896. *Houstonia xestosperma* (Robinson & Greenman) Terrell, Brittonia 32:493. 1980.

Distribution: México: Oaxaca.

Houstonia L., *Sp. Pl.* 1:105. 1753. Type species: *Houstonia caerulea* L.

Houstonia L. subg. *Houstonia*

1. *Houstonia caerulea* L., *Sp. Pl.* 1:105. 1753.

Partial synonymy follows:

Hedyotis caerulea (L.) Hook., *Fl. Bor.-Amer.* 1:286. 1833.

Houstonia linnaei Michx. var. *elatio*r Michx., *Fl. Bor.-Amer.* 1:84. 1803.

Houstonia caerulea L. var. *faxonorum* A.S. Pease & A.H. Moore, *Rhodora* 9:210. 1907.

Distribution: Eastern Canada: Nova Scotia, New Brunswick, and Quebec; Eastern U.S. (excluding Florida), west to northeastern Mississippi, northern Louisiana, Arkansas, southern Missouri, eastern Iowa, and southern Wisconsin.

2. *Houstonia micrantha* (Shinners) Terrell, *Phytologia* 31:425. 1975.
Hedyotis crassifolia Raf. var. *micrantha* Shinners, *Field & Lab.* 18:100. 1950, non *Hedyotis micrantha* Hochst. ex Hiern 1877.

Hedyotis australis W.H. Lewis & D.M. Moore, *Southw. Naturalist* 3:208. 1959, non *Houstonia australis* I.M. Johnston 1922.

Distribution: U.S.: Centered in Louisiana, eastern Texas, and Arkansas, with extensions to southeastern Oklahoma, southwestern (Shelby Co.) Tennessee, Mississippi, Tuscaloosa Co. in central Alabama, and Bibb and Columbia cos. in Georgia.

3. *Houstonia procumbens* (Walter ex J.F. Gmel.) Standl., *N. Amer. Fl.* 32(1):26. 1918.

Partial synonymy follows:

BASIONYM: *Anonymos procumbens* Walter, *Fl. Carol.* 86. 1788, *nom. illeg.*; see Ward (1962). *Poiretia procumbens* (Walter) J.F. Gmel., *Syst. Nat.* 2:263. 1791. *Hedyotis procumbens* (J.F. Gmel.) Fosb., *Castanea* 19:32. 1954.

Houstonia rotundifolia Michx., *Fl. Bor.-Amer.* 1:85. 1803.

Hedyotis procumbens (J.F. Gmel.) Fosb. var. *hirsuta* W.H. Lewis, *Ann. Missouri Bot. Gard.* 53:378. 1966.

Distribution: U.S.: Atlantic and Gulf Coastal Plains from eastern South Carolina to southern Florida, west to southern Alabama, Mississippi, and southeastern Louisiana.

4. *Houstonia pusilla* Schoepf, *Reise Nordamer. Staat.* 2:306. 1788.

Partial synonymy follows:

Houstonia linnaei Michx. var. *minor* Michx., *Fl. Bor.-Amer.* 1:85. 1803.

Houstonia patens Elliott, *Sketch Bot. S. Carolina* 1:191. 1816.

Hedyotis crassifolia Raf., *Fl. Ludov.* 77. 1817.

Houstonia minima Beck, *Amer. J. Sci.* 10:262. 1826.

Distribution: U.S.: Northern Maryland (adventive), central Virginia south to northwest Florida, west to central Texas, Oklahoma, Kansas, Missouri, eastern Iowa, Illinois, and Kentucky.

Comment: I have sunk *Houstonia minima* because of its considerable morphological intergradation with *H. pusilla* and its inconsistent geographical distribution.

5. *Houstonia rosea* (Raf.) Terrell, *Rhodora* 88:395. 1986. BASIONYM: *Hedyotis rosea* Raf., *Fl. Ludov.* 77. 1817.

Houstonia patens Elliott var. *pusilla* A. Gray, *Syn. Fl. N. Amer.* 1, 2:25. 1884. *Houstonia minor pusilla* (A. Gray) Small, *Fl. S.E. U.S.* 1107, 1338. 1903.

Houstonia pygmaea C.H. & M.T. Muller, *Bull. Torrey Bot. Club* 63:33. 1936, non *Hedyotis pygmaea* Roem. & Schult. 1818.

Hedyotis taylorae Fosb. in Shinnery, *Field & Lab* 17:169. 1949. (Author citation *fide* Fosberg personal commun.)

Distribution: U.S.: Mississippi, Louisiana, eastern Texas, eastern half of Oklahoma, Arkansas, southeastern Missouri, and Tuscaloosa Co. in central Alabama.

Comment: Terrell (1986a) discussed nomenclatural and taxonomic problems.

6. *Houstonia serpyllifolia* Michx., *Fl. Bor.-Amer.* 1:85. 1803.

Partial synonymy follows:

Hedyotis serpyllifolia (Michx.) Torr. & Gray, *Fl. N. Amer.* 2:39. 1841, non Poir. 1813.

Houstonia tenella Pursh, *Fl. Amer. Sept.* 106. 1814, non *Hedyotis tenella* Hochst. 1844.

Hedyotis michauxii Fosb., *Amer. Midl. Naturalist* 29:786. 1943.

Distribution: Centered in Blue Ridge Mountains in North Carolina, Tennessee, adjacent Georgia, South Carolina, and southwestern Virginia, extending to southeastern Kentucky, West Virginia, Garrett Co., Maryland, and Somerset Co., Pennsylvania. Usually at altitudes above 3000 ft. or in cool, protected places at lower altitudes.

Houstonia subg. *Chamisme*

Houstonia subg. *Chamisme* Raf., Ann. Gen. Sci. Phys. 5:227. 1820. Type species: *Houstonia purpurea* L.

1. *Houstonia canadensis* Willd. ex Roem. & Schult., *Syst. Veg.* 3:527. 1818.

Partial synonymy follows:

Hedyotis canadensis (Willd.) Fosb., Virginia J. Sci. 2:110. 1941.
Houstonia ciliolata Torr., *Fl. N. Middle United States* 1:173. 1824.
Houstonia setiscaphia L.G. Carr, *Rhodora* 46:309. 1944. *Hedyotis purpurea* (L.) Torr. & Gray var. *setiscaphia* (L.G. Carr) Fosb., *Castanea* 19:35. 1954. *Houstonia canadensis* Willd. ex Roem. & Schult. var. *setiscaphia* (L.G. Carr) C.F. Reed, *Phytologia* 63:412. 1987.

Distribution: Canada: Ontario: Manitoulin Island, Bruce Peninsula, and locally in southern Ontario; U.S.: southward through western New York, Michigan, Ohio, southwestern Pennsylvania and adjacent West Virginia, southern Indiana, Kentucky, southwestern Virginia, Tennessee, to northwestern Georgia.

Comments: *Houstonia setiscaphia*, occurring in cedar glades in Lee Co., Va., was studied in the field by Terrell (1959). It intergrades strongly with the nearest populations in Virginia, Kentucky, and Tennessee, and is not varietally distinct.

2. *Houstonia longifolia* Gaertn., *Fruct. Sem. Pl.* 1:226. Tab. XLIX. 1788.

2a. *Houstonia longifolia* Gaertn. var. *longifolia*

Partial synonymy follows:

Hedyotis longifolia (Gaertn.) Hook., *Fl. Bor.-Amer.* 1:286. 1833.
Houstonia longifolia Gaertn. var. *compacta* Terrell, *Rhodora* 61:202. 1959.
Houstonia longifolia Gaertn. var. *glabra* Terrell, *Rhodora* 61:204. 1959.

Houstonia longifolia Gaertn. var. *musci* Boivin, *Phytologia* 16:29. 1968.

Houstonia longifolia Gaertn. var. *soperi* Boivin, *Phytologia* 16:30. 1968.

Distribution: Canada: southern Ontario and west to Manitoba, Saskatchewan, and Alberta; U.S.: New England and Great Lakes region to North Dakota; from New England south to southwestern Georgia, Alabama, and locally in Mississippi; Ozarks and Ouachitas in Arkansas, eastern Oklahoma, Missouri, and southern Illinois; sporadically in northern Illinois and Indiana.

Comments: My own and Boivin's varieties are here sunk because of the complex variation in the species, to be discussed elsewhere.

2b. *Houstonia longifolia* Gaertn. var. *tenuifolia* (Nutt.) A. Wood, *Class-book Bot.*, ed. 1861. 403. 1861.

Partial synonymy follows:

BASIONYM: *Houstonia tenuifolia* Nutt., *Gen. N. Amer. Pl.* 1:95. 1818, non *Hedyotis tenuifolia* Sm. 1811. *Hedyotis longifolia* (Gaertn.) Hook. var. *tenuifolia* (Nutt.) Torr. & Gray, *Fl. N. Amer.* 2:40. 1841. *Oldenlandia purpurea* (L.) A. Gray var. *tenuifolia* (Nutt.) Chapm., *Fl. Southern U.S.* 181. 1860.

Hedyotis nuttalliana Fosb., *Virginia J. Sci.* 2:111. 1941.

Distribution: U.S.: Local, mostly in Appalachians and Piedmont from northwestern Virginia to northwestern Florida, intergrading locally with var. *longifolia*.

Comment: I agree with Smith's (1976) statement that *Houstonia tenuifolia* cannot be maintained as a species. Varieties *longifolia* and *tenuifolia* intergrade strongly, as shown by data to be provided in a later publication.

3. *Houstonia ouachitana* (E.B. Sm.) Terrell, *Phytologia* 65:119. 1988.

BASIONYM: *Hedyotis ouachitana* E.B. Sm., *Brittonia* 28:457. 1976.

Distribution: U.S.: Arkansas: Howard, Little River, Montgomery, Polk, and Scott counties; Oklahoma: Leflore and McCurtain counties.

Comment: During field work in 1986 I found that this species does not intergrade with *Houstonia longifolia* sens. lat., although it closely resembles *H. longifolia* var. *tenuifolia*.

4. *Houstonia purpurea* L., *Sp. Pl.* 1:105. 1753.4a. *Houstonia purpurea* L. var. *purpurea*

Partial synonymy follows:

Hedyotis purpurea (L.) Torr. & Gray, *Fl. N. Amer.* 2:40. 1841.*Oldenlandia purpurea* (L.) A. Gray, *Manual*, ed. 2. 173. 1856.

Distribution: Southeastern U.S. (excluding Florida), west to east central (Newton Co.) Texas, eastern Oklahoma, southwestern Missouri, southern parts of Illinois, Indiana, and Ohio (where intergrading with var. *calycosa*), to West Virginia, Fayette Co., Pennsylvania, Maryland, and Delaware.

4b. *Houstonia purpurea* L. var. *calycosa* A. Gray, *Syn. Fl. N. Amer.* 1(2):26. 1884.

Partial synonymy follows:

Hedyotis calycosa A. Gray, *Pl. Wright.* 1:81. 1852, pro syn.*Houstonia calycosa* (A. Gray) C. Mohr, *Contr. U.S. Natl. Herb.* 6:739. 1901. *Hedyotis purpurea* (L.) Torr. & Gray var. *calycosa* (A. Gray) Fosb., *Castanea* 19:33. 1954.*Hedyotis lanceolata* Poir. in Lam., *Encycl.*, Suppl. 3:14. 1813.*Houstonia lanceolata* (Poir.) Britton, *Man. Fl. N. States* 861. 1901.

Distribution: U.S.: Primarily west of the Appalachians, most distinct in the cedar glades of Tennessee and Alabama, sporadically elsewhere, north to southern parts of Ohio, Indiana, and Illinois, west to eastern Oklahoma and southwestern Missouri; also adventive locally in New England.

Comment: Although distinct in its extremes, it intergrades strongly with var. *purpurea* (see also Terrell 1959).

4c. *Houstonia purpurea* L. var. *montana* (Small) Terrell, *Rhodora* 61:169. 1959. BASIONYM: *Houstonia montana* Small, *Fl. S.E. U.S.* 1325. 1903. *Hedyotis purpurea* (L.) Torr. & Gray var. *montana* (Small) Fosb., *Castanea* 19:33. 1954.

Distribution: U.S.: Occurring at altitudes of 6000 ft. and above on summits of Roan Mountain (Mitchell Co., N.C. and Carter Co., Tenn.) and Grandfather Mountain (Avery and Watauga cos., N.C.). Absent from other high mountains in the Blue Ridge, but recent collections from Bluff Mountain, Ashe County, N.C., are morphologically similar to var. *montana* and need further study.

Comments: The status of this taxon was discussed by Terrell (1959, 1978) and Yelton (1974).

Houstonia subg. *Ericotis* Terrell

1. *Houstonia acerosa* (A. Gray) Benth. & Hook. f., *Gen. Pl.* 2:60. 1873.
 - 1a. *Houstonia acerosa* (A. Gray) Benth. & Hook. f. subsp. *acerosa*
 BASIONYM: *Hedyotis acerosa* A. Gray, *Pl. Wright.* 1:81. 1852.
Oldenlandia acerosa (A. Gray) A. Gray, *Pl. Wright.* 2:67. 1853.
Mallostoma acerosa (A. Gray) Hemsl., *Biol. Centr.-Amer., Bot.*
 2:31. 1881. *Ereicottis acerosa* (A. Gray) Kuntze, *Rev. Gen. Pl.*
 1:281. 1891, orth. error for *Ereicotis* (see note under subgenus).

Distribution: U.S.: Western Texas; México: southwestern Tamaulipas, Nuevo León, San Luis Potosí, Coahuila.

- 1b. *Houstonia acerosa* (A. Gray) Benth. & Hook. f. subsp. *polypremoides*
 (A. Gray) Terrell, *Brittonia* 31:168. 1979. BASIONYM: *Houstonia polypremoides* A. Gray, *Proc. Amer. Acad. Arts* 21:379. 1886.
Hedyotis polypremoides (A. Gray) Shinnery, *Field & Lab.* 17:168. 1949.
Hedyotis acerosa A. Gray var. *polypremoides* (A. Gray) W.H. Lewis, *Ann. Missouri Bot. Gard.* 55:31. 1968.
Houstonia polypremoides A. Gray var. *bigelovii* Greenm., *Proc. Amer. Acad. Arts* 32:291. 1897. *Hedyotis acerosa* A. Gray var. *bigelovii* (Greenm.) W.H. Lewis, *Ann. Missouri Bot. Gard.* 55:397. 1969.

Distribution: U.S.: Southwestern Texas, New Mexico. México: Coahuila, Chihuahua.

2. *Houstonia correllii* (W.H. Lewis) Terrell, *Phytologia* 31:425. 1975.
 BASIONYM: *Hedyotis correllii* W.H. Lewis, *Brittonia* 24:395-397. 1972.

Distribution: U.S.: Texas (Zapata Co. in Rio Grande Valley).

Comment: In 1990 we found this species only at the type locality; it must be considered very rare.

3. *Houstonia croftiae* Britton & Rusby, *Trans. New York Acad. Sci.* 7:10. 1887. *Hedyotis croftiae* (Britton & Rusby) Shinnery, *Field & Lab.* 17:167. 1949.

Distribution: U.S.: Southeastern Texas.

4. *Houstonia humifusa* (A. Gray) A. Gray, *Proc. Amer. Acad. Arts* 4:314. 1859. BASIONYM: *Hedyotis humifusa* A. Gray, *Boston J. Nat. Hist.* 6:216. 1850. *Oldenlandia humifusa* (A. Gray) A. Gray, *Pl. Wright.* 2:68. 1853.

Distribution: U.S.: Texas, New Mexico, western Oklahoma.

5. *Houstonia palmeri* A. Gray, Proc. Amer. Acad. Arts 17:202. 1882.
Hedyotis palmeri (A. Gray) W.H. Lewis, Rhodora 63:222. 1961.

Houstonia longipes S. Watson, Proc. Amer. Acad. Arts 18:97.
1883. *Hedyotis longipes* (S. Watson) W.H. Lewis, Rhodora
63:222. 1961.

Distribution: México: Nuevo León, San Luis Potosí, Coahuila.

Comment: The type specimens of *Houstonia palmeri* and *H. longipes* were collected at different developmental stages, but are conspecific.

6. *Houstonia parviflora* Holzinger ex Greenm., Proc. Amer. Acad. Arts
32:284. 1897, non *Hedyotis parviflora* Walpers 1852.

Hedyotis greenmanii Fosb. in Shinnery, Field & Lab. 17:167. 1949.
(Citation fide Fosberg commun.).

Distribution: U.S.: southern and southcentral Texas.

7. *Houstonia rubra* Cav., Icon. 5:48, t. 474, f. 1. 1799. *Hedyotis
rubra* (Cav.) A. Gray, Mem. Amer. Acad. Arts n.s. 4:61. 1849.
Oldenlandia rubra (Cav.) A. Gray, Pl. Wright. 2:68. 1853.

Houstonia saxicola Eastwood, Proc. California Acad. Sci., ser. 2,
6:291. 1896.

Distribution: U.S.: Western Texas, New Mexico, Arizona, southeastern Utah; México: North and central.

8. *Houstonia spellenbergii* (Nesom & Vorobik) Terrell, *comb. nov.*
BASIONYM: *Hedyotis spellenbergii* Nesom & Vorobik, Syst. Bot.
13:432. 1988.

Distribution: México: West central Chihuahua.

9. *Houstonia subviscosa* (Wright ex A. Gray) A. Gray, Proc. Amer.
Acad. Arts 4:314. 1859. BASIONYM: *Oldenlandia subviscosa*
Wright ex A. Gray, Pl. Wright. 2:68. 1853. *Hedyotis subviscosa*
(Wright ex A. Gray) Shinnery, Field & Lab. 17:169. 1949.

Distribution: U.S.: Eastern Texas, especially in southeast.

10. *Houstonia wrightii* A. Gray, Proc. Amer. Acad. Arts 17:202. 1882.
Hedyotis wrightii (A. Gray) Fosb., Lloydia 4:290. 1941.

Hedyotis pygmaea Roem. & Schult., *Syst. Veg.* 3:526. 1818, non *Houstonia pygmaea* C.H. & M.T. Muller 1936.

Hedyotis pumila Willd. ex Roem. & Schult., *Syst. Veg.* 3:526. 1818, *nom. illeg.*, as synonym of *H. pygmaea*; non *H. pumila* L.

Hedyotis cervantesii H.B.K., *Nov. Gen. Sp.* 3:390. 1820, *nom. illeg.*; see Terrell 1988. *Anotis cervantesii* (H.B.K.) DC., *Prodr.* 4:432. 1830. *Ereicocotis cervantesii* (H.B.K.) Kuntze, *Rev. Gen. Pl.* 1:281. 1891, orth. error (see under subgenus).

Distribution: U.S.: Southwestern Texas, New Mexico, Arizona; México: North and central.

Oldenlandia L., *Sp. Pl.* 1:119. 1753.

1. *Oldenlandia boscii* (DC.) Chapm., *Fl. Southern U.S.* 181. 1860. BASIONYM: *Hedyotis boscii* DC., *Prodr.* 4:420. 1830.

Distribution: U.S.: Mainly in the Atlantic and Gulf Coastal Plains and Mississippi Embayment in the southeastern states, also in the Ozark region. Southeastern Virginia, one county in southeastern North Carolina, South Carolina, southwestern and one county in northern Georgia, northern Florida, west to eastern parts of Texas and Oklahoma, Arkansas, southeastern Missouri, north to central and west Tennessee.

2. *Oldenlandia corymbosa* L., *Sp. Pl.* 1:119. 1753. *Hedyotis corymbosa* (L.) Lam., *Tabl. Encycl.* 1:272. 1792.

Distribution: Pantropic weed. U.S.: Mainly in Atlantic and Gulf Coastal Plains and Mississippi Embayment. Eastern South Carolina, southern Georgia, throughout Florida, southern parts of Alabama, Mississippi and Louisiana, and rare in eastern Texas; Hawaii: Oahu, Hawaii, and Maui. México: Nayarit, Tabasco, Chiapas, and probably elsewhere.

3. *Oldenlandia drymarioides* (Standley) Terrell, *Phytologia* 59:80. 1985. BASIONYM: *Houstonia drymarioides* Standley, *J. Washington Acad. Sci.* 18:162. 1928. *Hedyotis drymarioides* (Standley) W.H. Lewis, *Rhodora* 63:221. 1961.

Distribution: México: Tamaulipas.

4. *Oldenlandia lancifolia* (Schumacher) DC., *Prodr.* 4:425. 1830. BASIONYM: *Hedyotis lancifolia* Schumacher, *Beskr. Guin. Pl.* 72. 1827.

Distribution: Tropical Africa. Introduced or adventive in México: Tamaulipas, Veracruz, Oaxaca, Chiapas, and Tabasco. Also in Central America, West Indies, and South America. Reports of *Oldenlandia herbacea* L. from the Western Hemisphere by Standley (1918) and others were probably mostly or entirely misidentifications of *O. lancifolia*.

5. *Oldenlandia microtheca* (Schlecht. & Cham.) DC., *Prodr.* 4:428. 1830. BASIONYM: *Gerontogea microtheca* Schlecht. & Cham., *Linnaea* 5:169. 1830. *Hedyotis microtheca* (Schlecht. & Cham.) Steud., *Nomencl. Bot.*, ed. 2. 1:728. 1840.

Gerontogea deppeana Schlecht. & Cham., *Linnaea* 5:169. 1830.
Oldenlandia deppeana (Schlecht. & Cham.) DC., *Prodr.* 4:428. 1830. *Hedyotis deppeana* (Schlecht. & Cham.) Steud., *Nomencl. Bot.*, ed. 2. 1:727. 1840.

Distribution: México: San Luis Potosí, Hidalgo, Puebla, Veracruz. Standley (1918) listed Yucatán, but I have not seen any specimens from there.

6. *Oldenlandia ovata* S. Watson, *Proc. Amer. Acad. Arts* 18:97. 1883, non *Hedyotis ovata* Thunb. ex Maxim., *Bull. Acad. Imp. Sci. Saint-Petersbourg* 29:161. 1883.

Hedyotis watsonii W.H. Lewis, *Rhodora* 63:222. 1961.

Distribution: México: Nuevo León and Tamaulipas south to San Luis Potosí and Hidalgo.

7. *Oldenlandia pringlei* B.L. Robinson, *Proc. Amer. Acad. Arts* 27:169. 1892. *Hedyotis pringlei* (B.L. Robinson) W.H. Lewis, *Rhodora* 63:222. 1961.

Distribution: México: San Luis Potosí.

8. *Oldenlandia salzmännii* (DC.) Benth. & Hook. f. ex B.D. Jacks., *Index Kew.* 2:336. 1894; Benth. & Hook. f., *Gen. Pl.* 2:58. 1873, ined. (see Fosberg & Terrell 1985). *Anotis salzmännii* DC., *Prodr.* 4:433. 1830. *Hedyotis salzmännii* (DC.) Steud., *Nomencl. Bot.*, ed. 2. 1:726. 1840.

Hedyotis thesiifolia A. St. Hil., *Voy. Distr. Diam.* 1:397. 1833.
Oldenlandia thesiifolia (A. St. Hil.) K. Schum. in Mart., *Fl. Bras.* 6, 6:270. Pl. 127, f. 1. 1889.

Distribution: South America: Brazil, Argentina, Uruguay, and Paraguay. U.S.: Locally established, apparently accidentally, near Pensacola, Escambia Co., western Florida, and in adjacent Baldwin Co., Alabama, where discovered by J.R. Burkhalter of Pensacola (Fosberg & Terrell 1985).

9. *Oldenlandia uniflora* L., *Sp. Pl.* 1:119. 1753. *Hedyotis uniflora* (L.) Lam., *Tabl. Encycl.* 1:272. 1792.

Other synonyms listed by Terrell (1990).

Distribution: U.S.: Mainly in Atlantic and Gulf Coastal Plains and Mississippi Embayment. Southeastern U.S. to southern Florida, west to eastern parts of Texas and Oklahoma, southern Arkansas, southeastern Missouri, north to western Kentucky, western Tennessee, Maryland (southeast and Prince Georges Co.), District of Columbia, Delaware, New Jersey, and Long Island in New York. Also occurs in West Indies in Cuba, Puerto Rico, and Jamaica.

Oldenlandiopsis (Griseb.) Terrell & W.H. Lewis, *Brittonia* 42:185. 1990. One species.

Oldenlandiopsis callitrichoides (Griseb.) Terrell & W.H. Lewis, *Brittonia* 42:185. 1990. BASIONYM: *Oldenlandia callitrichoides* Griseb., *Mem. Amer. Acad. Arts* n.s. 8:506. 1863. *Hedyotis callitrichoides* (Griseb.) W.H. Lewis, *Rhodora* 63:222. 1961.

Distribution: West Indies; Central America; México (Yucatán); adventive in Africa (Sierra Leone); northern South America (Guyana); United States: Dade County, Florida; Hawaii.

Pentodon Hochst., *Flora* 27:552. 1844. Two African species, incl. *P. pentandrus*. Partial synonymy; see also Verdcourt (1976), Rogers (1987).

Pentodon pentandrus (Schumach. & Thonn.) Vatke, *Oest. Bot. Zeitschr.* 25:231. 1875. BASIONYM: *Hedyotis pentandra* Schumach. & Thonn., *K. Danske Vid. Selsk. Nat. Math. Afh.* 3:71. 1827. *Oldenlandia pentandra* (Schumach. & Thonn.) DC., *Prodr.* 4:427. 1830, non Retz.

Hedyotis halei Torr. & Gray, *Fl. N. Amer.* 2:42. 1841. *Oldenlandia halei* (Torr. & Gray) Chapm., *Fl. Southern U.S.* 181. 1860. *Pentodon halei* (Torr. & Gray) A. Gray, *Syn. Fl. N. Amer.* 1, 2:28. 1884.

Distribution: Africa. U.S.: Coastal plain, South Carolina to Florida, west to Arkansas, Louisiana, and eastern Texas.

SUMMARIZED LIST OF ACCEPTED SPECIES

Carterella Terrell

- C. alexanderiae* (A. Carter) Terrell (*Hedyotis* a. [A. Carter] W.H.Lewis)-
Mex.: B.C.

Hedyotis L.

- H. angulata* Fosb. (*Houstonia rupicola* Greenm.)-U.S.: sw Texas; n Mex.
H. arenaria (Rose) W.H. Lewis-Mex.: B.C.
H. asperuloides Benth.-Mex.: B.C.
H. brevipes (Rose) W.H. Lewis-Mex.: B.C.
H. butterwickiae (Terrell) Nesom-U.S.: Texas
H. galeottii (Martens) Terrell & Lorence-s Mex.
H. gracilentia (I.M. Johnston) W.H. Lewis-Mex.: B.C.
H. greenei (A. Gray) W.H. Lewis (*Oldenlandia* g. A. Gray)-U.S.: Ariz.
H. intricata Fosb. (*Houstonia fasciculata* A. Gray)-sw U.S.; n Mex.
H. kingii (Terrell) Nesom-Mex.: Oax.
H. latifolia (Martens & Galeotti) Walpers-Mex.: Ver., Chiap., Oax.; Guat.
H. mucronata Benth.-Mex.: B.C.
H. mullerae Fosb.-Mex.: Coah.
H. nigricans (Lam.) Fosb. var. *nigricans* (*Houstonia* n. [Lam.] Fern.; *H. angustifolia* Michx.; *H. salina* A.A. Heller; *H. tenuis* Small)-e to w U.S.; n to c Mex.
 H. nigricans (Lam.) Fosb. var. *floridana* (Standley) Wunderlin-U.S.: Fla.; Bahamas.
 H. nigricans (Lam.) Fosb. var. *pulvinata* (Small) Fosb.-U.S.: Fla.
H. peninsularis (Brandegee) W.H. Lewis-Mex.: B.C.
H. saxatilis W.H. Lewis (*Houstonia australis* I.M. Johnston)-Mex.: B.C.
H. sharpii (Terrell) Nesom-Mex.: Ver., Hgo.
H. teretifolia (Terrell) Nesom-Mex.: Coah.
H. umbratilis (B.L. Robinson) W.H. Lewis-n & c Mex.
H. vegrandis W.H. Lewis (*Houstonia prostrata* Brandegee)-nw Mex. & B.C.

H. xestosperma (Robinson & Greenman) W.H. Lewis-Mex.: Oax.

Houstonia L.

H. acerosa (A. Gray) Benth. & Hook. f. subsp. *acerosa*-sw U.S.; n Mex.

H. acerosa (A. Gray) Benth. & Hook. f. subsp. *polypremoides* (A. Gray) Terrell-sw U.S.; n Mex.

H. caerulea L.-e Can.; e & c U.S.

H. canadensis Willd. ex Roem. & Schult. (*H. ciliolata* Torr.; *H. setiscaphia* L.G. Carr)-Can.: Ont.; e & c U.S.

H. correllii (W.H. Lewis) Terrell-U.S.: Texas

H. croftiae Britton & Rusby-U.S.: Texas

H. humifusa (A. Gray) A. Gray-sw U.S.

H. longifolia Gaertn. var. *longifolia*-Can.; e & c U.S.

H. longifolia Gaertn. var. *tenuifolia* (Nutt.) A. Wood (*H. tenuifolia* Nutt.; *Hedyotis nuttalliana* Fosb.)-U.S.: Va. to Fla.

H. micrantha (Shinners) Terrell (*Hedyotis australis* W.H. Lewis & D.M. Moore)-sc & se U.S.

H. ouachitana (E.B. Sm.) Terrell-U.S.: Ark.

H. palmeri A. Gray (*H. longipes* S. Wats.)-n Mex.

H. parviflora Holzinger ex Greenm. (*Hedyotis greenmanii* Fosb.)-U.S.: Texas

H. procumbens (Walter ex J.F. Gmel.) Standley (*H. rotundifolia* Michx.)-se U.S. to La.

H. purpurea L. var. *purpurea*-e & c U.S.

H. purpurea L. var. *calycosa* A. Gray (*H. lanceolata* (Poir.) Britton)-Mainly c U.S.

H. purpurea L. var. *montana* (Small) Terrell (*H. montana* Small)-w N.C., e Tenn.

H. pusilla Schoepf (*H. minima* Beck; *H. patens* Ell.; *Hedyotis crassifolia* Raf.)-e & c U.S.

H. rosea (Raf.) Terrell (*H. pygmaea* C.H. & M.T. Muller)-sc & se U.S.

H. rubra Cav. (*H. saxicola* Eastwood)-sw U.S.; n & c Mex.

H. serpyllifolia Michx. (*H. tenella* Pursh; *Hedyotis michauxiana* Fosb)-U.S.: Ga., S.C. to sw Pa.

H. spellenbergii (Nesom & Vorobik) Terrell-Mex.: Chih.

H. subviscosa (Wright ex A. Gray) A. Gray-U.S.: Texas

H. wrightii A. Gray (*Hedyotis pygmaea* Roem. & Schult.; *H. cervantesii* H.B.K.)—sw U.S.; n & c Mex.

Oldenlandia L.

O. boscii (DC.) Chapm.—se & sc U.S.

O. corymbosa L.—se & sc U.S., Hawaii; Mex.

O. drymarioides (Standley) Terrell—Mex.: Tam.

O. lancifolia (Schumacher) DC.—Mex.

O. microtheca (Schlecht. & Cham.) DC.—Mex.: mainly ec

O. ovata S. Watson (*Hedyotis watsonii* W.H. Lewis) Mex.: ne to Hgo.

O. pringlei B.L. Robinson—Mex.: S.L.P.

O. salzmännii (DC.) Benth. & Hook. f. ex B.D. Jacks.—S. Amer.; U.S.: Fla., Ala.

O. uniflora L.—Mainly se & sc U.S., W.I.

Oldenlandiopsis Terrell & W.H. Lewis

O. callitrichoides Terrell & W.H. Lewis—W.I., C. Am., Mex.; U.S.: Fla.

Pentodon Hochst.

P. pentandrus (Schumach. & Thonn.) Vatke—Africa; se U.S.

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REDEFINITION OF *HESPERODORIA* (ASTERACEAE: ASTEREA) AND
THE SEGREGATION OF *COLUMBIADORIA*, A NEW MONOTYPIC GENUS
FROM THE WESTERN UNITED STATES

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ABSTRACT

The genus *Hesperodoria* is ditypic with the inclusion of *Hesperodoria salicinus* *comb. nov.* This species, which is endemic to northern Arizona, has not formerly been treated outside of *Haplopappus*. *Hesperodoria scopulorum* occurs in northern Arizona and southern Utah. The only other species to have been included in *Hesperodoria* is here described as a monotypic genus, *Columbiadoria*, with the new combination *Columbiadoria hallii*. This species occurs in Oregon and Washington, and has been placed in *Haplopappus*, *Pyrrocoma*, *Aster*, and *Hoorebekia*. Both *Hesperodoria* and *Columbiadoria* are members of the *Petradoria* group of the Solidagininae, although they are not closely related to each other within it. A key distinguishes both species of *Hesperodoria* along with those of *Petradoria*, *Vancleavea*, and *Stenotus*, the genera most similar to *Hesperodoria*. The phylogenetic position of *Columbiadoria* apparently is near *Tonestus*.

KEY WORDS: *Haplopappus*, *Columbiadoria*, *Hesperodoria*, Asteraceae, Astereae, Solidagininae

In a summary of the disposition of the North American segregates of *Haplopappus* (Nesom & Morgan 1990), the taxonomic status of the genus *Hesperodoria* E. Greene was noted to be poorly understood. The type species, *Hesperodoria scopulorum* (M.E. Jones) E. Greene is a relatively well known plant from northern Arizona and southern Utah. Another species, *Haplopappus salicinus* S.F. Blake, although clearly similar to *Hesperodoria*, was not assigned to a genus outside of *Haplopappus* because it was known to us only from the relatively immature specimens of the type collection. Recent material available for study, however, has clarified the identity of this species, and it is here transferred to *Hesperodoria*.

Hesperodoria salicinus (S.F. Blake) Nesom, *comb. nov.* BASIONYM: *Aplopappus salicinus* S.F. Blake, Proc. Biol. Soc. Washington 48:171. 1935. TYPE: UNITED STATES. Arizona. [Coconino Co.], Bright Angel Trail, Grand Canyon, 22 Oct 1905, A. Eastwood 10 (HOLOTYPE: US!).

As noted by Blake (1935) in the original description of *Haplopappus salicinus*, Hall (1928) cited the type (*Eastwood 10*) as a specimen of *H. scopulorum*. I have studied the type as well as a more recent, mature and ample collection of *H. salicinus*: United States. Arizona: Mojave Co., above S shore of Lake Mead, 26 Oct 1973, Martin & Van Devender s.n. (NY). Duplicates of this collection were distributed as "*Haplopappus cf. acradenus*." A more detailed study and taxonomic treatment of *Hesperodoria* is now being undertaken (Gary Baird in prep.).

Hesperodoria possesses a suite of characters that identify it as a member of the subtribe Solidagininae Hoffm., as outlined by Nesom (1991b). Within the subtribe, it is a part of the "*Petradoria* group," which comprises *Petradoria* E. Greene, *Vanclevea* E. Greene, *Hesperodoria*, *Stenotus* Nutt., *Tonestus* A. Nelson, *Columbiadoria* Nesom (see below), *Eastwoodia* Brandege, *Acamp-topappus* A. Gray, and *Amphipappus* Torr. & Gray. Taxonomic studies or overviews of a number of these genera are available (Porter 1943; Anderson 1963; Anderson & Weberg 1974; Lane 1988; Nesom & Morgan 1990; Nesom 1991a).

The taxa of the *Petradoria* group are confined to the western United States, except for *Stenotus*, which has one species endemic to Baja California, another that reaches into western Canada, and one endemic to Canada. Seven genera of the group are monotypic or ditypic; *Stenotus* and *Tonestus* have six and nine species, respectively. Within the Solidagininae, the *Petradoria* group can be recognized by its style appendages, which have massively thickened vascular traces, except in *Petradoria*, *Vanclevea*, *Columbiadoria*, and a few species of *Stenotus* and *Tonestus*, where the traces are not so massively thickened. The vascular traces of the style shaft are mostly 3-5 cells wide and maintain this width as they enter the style branches. Upon entering the appendages, however, each trace abruptly widens to 15-20 cells, forming a distinctly clavate terminal portion. This feature apparently does not occur in any other American Astereae.

Hesperodoria is most closely similar to *Petradoria* (in line with Greene's original assessment and in contradiction to Hall's reassessment) and to *Vanclevea*. The plants of these three genera are herbs or small subshrubs that produce coriaceous, linear to linear lanceolate leaves with three(-five), parallel, raised veins; the leaves are mostly punctate-glandular, and the margins and lamina are glabrous or sometimes hirtellous-scabrous. Anderson & Weberg (1974) found that the leaves of these taxa are similar in their isolateral

mesophyll and massive sclerenchymatous bundle sheaths that completely surround the vascular tissue. The capitulescences are mostly cymose, the ray flowers absent or with short ligules. *Petradoria* and *Vancleavea* both have a chromosome base of $x = 9$ (Anderson 1963, Anderson & Weberg 1974) but there is no documented report for either species of *Hesperodoria*. All other chromosome numbers reported for plants of the *Petradoria* group are also on a base of $x = 9$, and the same is predicted for those species yet unstudied.

As noted above, *Petradoria* and *Vancleavea* both lack the massively thickened vascular traces of the disc style appendages that are characteristic of almost all of the rest of the *Petradoria* group, including *Hesperodoria*. Also, the disc corolla lobes of both genera are deltate rather than long-lanceolate, although the lobes of *H. scopulorum* are variable in length and some are relatively short. *Petradoria* differs further from *Hesperodoria* in habit, capitulescence, head shape, and achene vestiture. *Vancleavea* differs further from *Hesperodoria* in its attenuate phyllary apices and pappus of broad, strongly flattened awns. Of the two, however, *Vancleavea* is more similar to *Hesperodoria* in its habit, capitulescence, and head shape.

Anderson (1963) observed that the sclerenchymatous bundle sheaths of *Stenotus* are similar to those of *Petradoria* and *Hesperodoria*. This is true in both *Stenotus acaulis* (Nutt.) Nutt., the species studied by Anderson, and *S. armerioides* Nutt., but the foliar venation of the other species is not so conspicuously sclerified and raised. Further, although the major foliar veins in all species of *Stenotus* are parallel, the interconnecting veins tend to be much more prominent than in *Hesperodoria*, *Petradoria*, and *Vancleavea*. If *Stenotus* is a fourth member of this group, as seems likely, the other three genera are more similar among themselves in their leaf morphology, polycephalous capitulescence, and extreme reduction of the ray flowers.

In the present treatment, the genus *Hesperodoria* comprises two species, although yet another species was originally referred to it by Greene (see below, "A new monotypic genus"). The similarities and differences between *H. scopulorum* and *H. salicinus*, as well as among all the species of *Vancleavea* and *Petradoria*, are summarized in the key below. The two species of *Hesperodoria* are very different from each other, particularly in their glandularity and head, flower, and fruit size, so much so that in this taxonomic region of monotypic and ditypic genera, I originally thought that they might be better classified as two separate genera. They are more similar between themselves, however, than to any other species. The large difference between them is paralleled by that between the two species of *Petradoria*. Despite marked disparities among all five species of these three genera, they are morphologically and geographically similar among themselves and so clearly distinct as a group that they might be combined into a single genus. On the other hand, until additional lines of evidence might show otherwise, they may be justifiably distinguished as the taxa in the key below.

KEY TO THE TAXA MOST CLOSELY RELATED TO *HESPERODORIA*

1. Heads solitary; ray flowers with conspicuous ligules (except *Stenotus pulvinatus*). *Stenotus*
1. Heads more than one, mostly in flat topped capitulescences; ray flowers absent or if present, with very inconspicuous ligules. (2)
 2. Above ground stems annual or perennial; heads turbinate to cylindric; disc corolla lobes deltate, shallowly cut; vascular trace of disc style branches narrow, unthickened; ray flowers present or absent; pappus bristles apically narrowed, dilated in one species. (4)
 2. Above ground stems perennial, the basal portions woody; heads turbinate, disc corolla lobes narrowly triangular, deeply cut; vascular trace of disc style branches massively thickened; ray flowers absent; pappus bristles apically dilated. (3) *Hesperodoria*
3. Leaves ascending, eglandular and not resinous, the margins scabrous, the lamina glabrous or scabrous; heads 6-10 mm high, sessile to subsessile or on pedicels up to 1 cm long; (1-)3-5 in a cymose capitulescence; disc corollas 5-7 mm long, with lobes cut $\frac{1}{3}$ - $\frac{1}{2}$ the length of the limb; phyllaries slightly convex, with a glandular midline from base to tip, without a strongly developed apical glandular area; achenes 4 mm long, 6-8 nerved; northern Arizona and southern Utah.
..... *Hesperodoria scopulorum*
3. Leaves spreading to deflexed, punctate-glandular and resinous, glabrous; heads 4-5 mm high, on pedicels 2-5 mm long, numerous in a number of barely cymoid clusters, these associated in a loose panicle; disc corollas 2.8-3.2 mm long, with lobes cut to the base of the limb; phyllaries strongly convex, without a glandular midline but with a glandular apex; achenes 1 mm long, 5 nerved; northern Arizona.
..... *Hesperodoria salicinus*
4. Above ground stems perennial, the basal portions woody; leaves arcuate; heads turbinate, 9.5-12.5 mm high, solitary or 2-5 and loosely cymoid; phyllary apices attenuate; ray flowers absent; achenes sparsely strigose; pappus of broad, strongly flattened, linear-lanceolate awns; northern Arizona and southern Utah.
..... *Vancleavea stylosa*
4. Above ground stems annual, the basal portions mostly herbaceous; leaves ascending; heads cylindric, usually in a dense flat topped capitulescence; phyllary apices rounded to obtuse; rays present or absent; achenes glabrous; pappus of capillary bristles.
..... (5) *Petradoria*

5. Leaves eglandular; heads 11-13 mm high; phyllaries slightly convex, apically truncate-apiculate; rays absent; disc flowers hermaphroditic, fully fertile, the corollas 9-12 mm long; pappus bristles strongly flattened, apically dilated; east central California and southern Nevada.
..... *Petradoria discoidea*
5. Leaves punctate-glandular; heads 5-9 mm high; phyllaries strongly convex, apically obtuse to acute; ray flowers present; disc flowers staminate, with abortive ovaries, the corollas 4- 6 mm long; pappus bristles terete, not apically dilated; southeastern California, Nevada, northern Arizona and New Mexico, Colorado, Utah, and southwestern Wyoming and Idaho.
..... *Petradoria pumila*

A new monotypic genus of Solidagininae

The original description of *Hesperodoria* E. Greene (1906) was only of two sentences regarding the type (*H. scopulorum*) and its putative relationship to *Petradoria* E. Greene. Greene included one other species in *Hesperodoria*, appended with the following comments, which completed the entire discussion of his new genus: "Along with this I place tentatively a type which remained in *Aplopappus* as I left it, that is [*Haplopappus hallii* A. Gray]. That this has rays while the type is rayless does not with me count for much; but the involucre are not quite the same, neither is the pappus, nor even the style-tips." The only other comments ever published regarding the relationship between the two species of *Hesperodoria* apparently have been those of Hall (1928), who included both species as sect. *Hesperodoria* (E. Greene) Hall of the genus *Haplopappus*. "This section comprises two relict species so unlike each other and each so distinct from those of any other group that little can be said as to their relationships" (p. 218). "The wide separation of this species [*Haplopappus hallii* A. Gray] from any other, both geographically and morphologically, probably means that its exact phylogenetic position never will be determined" (p. 221).

While *Haplopappus hallii* is clearly a member of the Solidagininae and a member of the *Petradoria* group, Hall's assessment of its isolated position was correct. It is not closely similar to any other species of the subtribe and is recognized here as a distinct, monotypic genus. The proposed generic name juxtaposes the geographic home of the species with "Doria," an early name for the goldenrod (*Solidago*).

Columbiadoria Nesom, *gen. nov.* TYPE: *Haplopappus hallii* A. Gray

Subfrutices perennes e basi maxime ramosi. Caules ad basim lignei 3-6 dm alti stricti plerumque non ramosi sub capitulescentia. Folia oblanceolata integra dictyophlebia redacta versus apicem caulis. Capitula cylindrici-turbinata 8-11 mm alta plerumque 5-10 in capitulescentia laxa spicata vel leniter cymoidea. Flores radii 5-8 corollis 6-10 mm longis. Flores discii lobis deltatis; appendices ramorum stylinorum lineis stigmaticis 5-6-plo longiores. Achae-
nia 4-5 mm longa 8-nervia moderate strigosa; setae pappi graciles teretes attenuatae ad apices.

Columbiadoria hallii (A. Gray) Nesom, *comb. nov.* *Haplopappus hallii* A. Gray, Proc. Amer. Acad. Arts 8:389. 1872. TYPE: UNITED STATES. Oregon, [Wasco Co.], bluffs of Columbia River at The Dalles, 1871, *E. Hall* 257 (HOLOTYPE: GH!). *Aster howellii* Kuntze [*nom. nov.*], Rev. 316. 1891. *Hesperodoria hallii* (A. Gray) E. Greene, Leaflet Bot. Observ. 1:175. 1906. *Hoorebekia hallii* (A. Gray) Piper, Contr. U.S. Natl. Herb. 11:560. 1906. *Pyrocoma hallii* (A. Gray) Howell, Fl. N.W. Amer. 1:299. 1900.

Perennial subshrubs with woody, highly branched bases, arising from a stout taproot. Stems 3-6 dm tall, strict, mostly unbranched below the capitulescence. Leaves eglandular or obscurely punctate-glandular, not resinous, sparsely scabrous-hispidulous, oblanceolate, entire, net veined, sessile and petiolate, ascending, the largest 2-5 cm long, 4-7(-11) mm wide, gradually reduced in size upwards. Heads cylindric-turbinate, 8-11 mm high, 5-15 or more in a loosely spicate to broadly and loosely cymoid capitulescence; phyllaries in 5-6 strongly graduated series, convex, lanceolate, slightly glutinous, with a green viscid apex, not keeled or slightly so on the upper half, the lower $\frac{2}{3}$ white indurated. Ray flowers 5-8, pistillate, fertile, the corollas yellow, 6-10 mm long, the ligules 6-7 mm long and ca. 2 mm wide, weakly if at all coiling. Disc flowers hermaphroditic, all fertile, the corollas 6-7 mm long, the lobes erect, deltate, cut ca. $\frac{1}{10}$ the length of the limb; style branches 1.5-2.0 mm long, the appendages 5-6 times longer than the stigmatic lines, with short, closely set sweeping hairs, these merely papillate near the apex, vascular traces of appendages barely thickened distally. Achenes 4-5 mm long, narrowly oblong, slightly compressed, 8 nerved, moderately strigose with stiff hairs; pappus bristles slender, terete, the apices attenuate.

The species primarily occurs in the eastern Columbia River Gorge in northern Oregon and southern Washington, but it also is found in scattered localities in the Cascade Mountains of Oregon to about 100 km south of the river. Cronquist (1955) noted that the southern populations, outside of the gorge, are variants perhaps deserving recognition at varietal rank.

Columbiadoria clearly is a member of the *Petradoria* group of the *Solidagininae*, based on the morphology of its disc style appendages and its disc corollas with the filaments inserted at midtube (Nesom 1991b). Its oblanceolate, net veined, little sclerified leaves contrast strongly with the linear-lanceolate, parallel veined leaves of *Hesperodoria*, as well as those of the closely related *Petradoria*, *Vanclevea*, and *Stenotus*. Among the genera of the *Petradoria* group, only *Tonestus* has obviously net veined leaves, and only *Tonestus* and *Stenotus*, besides *Columbiadoria*, have ray flowers with long, conspicuous ligules. Additionally, both *Columbiadoria* and *Tonestus* tend to produce a racemoid capitulescence, verging toward a narrowly cymoid one. This tendency is particularly noticeable in *T. aberrans* (A. Nels.) Nesom & Morgan and *T. graniticus* (Tiehm & Shultz) Nesom & Morgan, although in other *Tonestus*, the heads are usually solitary.

The features common to *Tonestus* and *Columbiadoria* appear to be unspecialized ones, since they are also found in at least some species of *Solidago*. Although the distinctive style branch morphology of the first two places them as members of the *Petradoria* group, they may be phylogenetically basal elements, independently derived within it. *Tonestus* is the only genus of either the *Petradoria* group or the *Gutierrezia* group that produces leaves with toothed margins (two species produce entire leaves); in this aspect of its foliar morphology, however, it is similar to *Solidago*, where the leaves characteristically are net veined and toothed. *Tonestus* also differs from *Columbiadoria* in its herbaceous above ground parts, leaves in persistent basal rosettes, stipitate glandular vestiture in most of the species, and strongly keeled phyllaries with prominently strongly glandular apices.

The genera *Eastwoodia*, *Acamptopappus*, and *Amphipappus* appear to constitute a lineage apart from *Columbiadoria* and the genera of the *Petradoria* group discussed above. *Eastwoodia* and *Acamptopappus* are similar in their solitary heads and the long, apically acute sweeping hairs of their disc style appendages. All three genera produce strongly flattened pappus bristles and uninerved leaves (Lane 1988).

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MORPHOLOGICAL DEFINITION OF THE *GUTIERREZIA* GROUP (ASTERACEAE: ASTEREEAE)

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ABSTRACT

A putatively monophyletic group of genera related to *Solidago* (*Gutierrezia*, *Gymnosperma*, *Thurovia*, *Amphiachyris*, *Bigelowia*, *Euthamia*, and *Xylothamia*) identified by molecular studies can also be recognized by a specialized morphological feature. The white rayed genus *Gundlachia* is added to this group on the basis of its overall morphology. The anther filaments of these taxa are inserted at the junction of the corolla tube and limb rather than well below the tube apex, as is most common in other Astereae. *Solidago sphacelata* Raf. and *S. discoidea* Ell., which have been segregated as the monotypic genera *Brachychaeta* and *Brintonia*, respectively, also have the distinctive tube-limb filament insertion. In habit, vestiture, leaf morphology, and capitulescence, however, these species, as well as their closest relatives, lie securely within the genus *Solidago*. The subtribe Solidagininae, which comprises the *Gutierrezia* lineage, *Solidago*, *Chrysoma*, and genera of the *Petradoria* group, is recognized by characteristically flat topped capitulescences, primarily yellow rays, and particularly by the distinctive morphology of the disc style appendages.

KEY WORDS: *Gutierrezia*, *Solidago*, *Brachychaeta*, *Brintonia*, *Gundlachia*, Asteraceae, Astereae, Solidagininae

The studies by Suh (1989) and Morgan (1990) of restriction site variation in chloroplast DNA of North American Astereae have identified two closely related groups of genera that have been designated as the "*Solidago* L. lineage" and "*Gutierrezia* Lag. lineage" (Nesom *et al.* 1990). Together, they comprise what can now be relatively clearly defined as the subtribe Solidagininae Hoffm. These plants, in turn, are most closely related within the tribe to the *Aster* L., *Heterotheca* Cass., and *Machaeranthera* Nees lineages, with the *Chrysothamnus* Nutt., *Baccharis* L., and *Erigeron* L. lineages yet more basal in phylogenetic position.

In an effort to identify morphological correlates of these major groups within the tribe, a detailed morphological survey has been conducted, encompassing over 320 species, including 80 American genera of Astereae and many of their subdivisions. Flowers and fruits of each species studied have been dissected and mounted on permanent slides. All vouchers are from LL,TEX; a list of these is deposited in the "*Gutierrezia* reprint folder" at TEX. All species of the North and Central American genera of the *Gutierrezia* and *Solidago* lineages discussed in the text have been studied in detail, except for the following: *Euthamia* (Nutt.) Nutt. ex Cass. (4 species), *Gundlachia* A. Gray (2 species), *Gutierrezia* (5 species), *Solidago* (16 species), and *Stenotus* Nutt. (4 species).

The Solidagininae *sensu stricto* possess a set of features that distinguish them from other Astereae: ray flowers few (or absent), with short, primarily yellow ligules, disc corolla lobes deeply cut, spreading-reflexing, and a uniseriate pappus. Further, the collecting appendages of the disc flower styles have a distinctive, diagnostic, but previously unrecognized morphology: the appendages vary in length (absolutely as well as relative to the stigmatic portions) but the sweeping hairs are more densely arranged than in related lineages of Astereae. The most proximal sweeping hairs are often long-spreading, sometimes appearing like a basal "tuft," but they are quickly reduced in length toward the apex, where they are typically no more than papillate extensions. Some species within *Gutierrezia*, *Xylothamia*, and *Tonestus* have linear appendages with consistently longer sweeping hairs, but these appear to be specializations within the group. The style appendages in the *Machaeranthera*, *Aster*, *Heterotheca*, and *Chrysothamnus* lineages have more widely spaced sweeping hairs that continue to the very apex relatively unreduced in length.

The morphology of the style branches of the bisexual disc florets has been considered to be one of the four defining features of the tribe Astereae (Grau 1977, p. 540). "Style branches are in cross section semi-orbicular and tipped with subulate to triangular appendages covered with collecting hairs. The basal part of these branches is margined with stigmatic lines." And (p. 541) "The only significant variation is in the length of the apical appendage, which may vary from shortly triangular to filiform." In the present paper, I present the first of two major disagreements with Grau's assertion that there is essentially no deviation among styles in the tribe.

The chromosome number of all the plants related to *Solidago* is on a base of $x = 9$, except for *Gutierrezia* and three other genera closely related to it: *Gutierrezia* ($x = 4$ and 5), *Gymnosperma* Less. ($n = 8$, probably based on $x = 4$), *Thurovia* Rose ($x = 5$), and *Amphiachyris* (DC.) Nutt. ($x = 4$ and 5).

The genera of the *Solidago* lineage are the following: *Solidago* (tentatively including *Brintonia* E. Greene, *Brachychaeta* Torr. & Gray, *Oreochrysum** Rydb., and *Oligoneuron* Small) and the genera of the "*Petradoria* group":

*Tonestus** A. Nels., *Stenotus*, *Petradoria** E. Greene, *Vanclevea* E. Greene, *Hesperodoria* E. Greene, *Eastwoodia** Brandeg., *Amphipappus** Torr. & Gray, *Acamptopappus** A. Gray, and *Columbiadoria* Nesom. Those taxa with an asterisk were identified as a monophyletic group in the molecular studies of Suh (1989) or Morgan (1990) or both; the others are added here on the basis of their morphological similarity. Additional comments regarding most of these genera and their morphological coherence are found in a companion paper to this one (Nesom 1991). The genus *Chrysoma* Nutt. is related to *Solidago* but its phylogenetic position is anomalous and discussed separately below. Additionally, the *Solidagininae* may need to be broadened to include a group of white rayed taxa currently treated within *Aster* L. sensu lato but that appear to be more closely related to *Solidago* (Nesom in prep.).

The studies by Suh (1989) and Suh & Simpson (1990), which were focused primarily on *Gutierrezia*, identified a monophyletic group of genera that constitute the *Gutierrezia* lineage: *Gutierrezia*, *Gymnosperma*, *Thurovia*, *Amphiachyris*, *Bigelowia* DC., and *Euthamia*. Additionally, a group of eight species formerly placed within *Ericameria* Nutt. was segregated as the genus *Xylothamia* Nesom *et al.* (Nesom *et al.* 1990), which is most closely related to *Euthamia* and a part of the *Gutierrezia* lineage. *Gutierrezia*, *Gymnosperma*, *Amphiachyris*, and *Thurovia* have been recognized by various authors as closely related (e.g., Shinnery 1950; Ruffin 1974; Suh & Simpson 1990). Lane (1982) also recognized the relationship and sharply refined the naturalness of the group by excluding the genus *Xanthocephalum* Willd.

One additional genus is added here to the seven identified by Suh as members of the *Gutierrezia* lineage: *Gundlachia* A. Gray, which comprises 6-7 species, all restricted to the Caribbean islands. Its species belong with the *Gutierrezia* lineage in every morphological respect except the color of its rays, which are white, probably as an evolutionary specialization from a yellow rayed ancestor (see below). Upon drying, the ray corollas of *Gundlachia* are more or less the same color as yellow-rayed taxa within the *Gutierrezia* group. *Thurovia* and several species of *Gutierrezia*, as well as species within *Solidago* and *Tonestus*, are also white rayed. The leaf anatomy of *Gundlachia* was observed by Anderson & Creech (1975) to be similar to that of *Euthamia*.

The results of the present morphological survey of American *Astereae* corroborate Suh's conclusions based on molecular data in regard to the taxa related to *Gutierrezia*. In addition to their molecular similarity, the genera of the *Gutierrezia* lineage have disc corollas shaped more or less like wine glasses, the limb expanding abruptly above the tube, with the anther filaments inserted at the junction of the tube and limb. This feature was documented by Kapoor & Beaudry (1966), who used it to justify the generic segregation of *Euthamia* and *Brachychaeta* Torr. & Gray (see below) from *Solidago*, where the filament insertion in many species occurs well below the apex of the tube. Anderson (1970) noted the similarity in this feature between *Bigelowia* and *Euthamia*,

and on the basis of this and other characters, including karyotype (Anderson 1977), he hypothesized that the two genera are closely related. Outside of the *Gutierrezia* group, filament insertion at the tube-limb junction occurs consistently only in some species of *Solidago* (including *Brachychaeta*, see below), which were not included in Suh's sample, and some taxa of the subtribe Baccharidinae.

Plants of the *Gutierrezia* lineage also are distinguished from those of the *Solidago* lineage by their glabrous or glabrate vestiture (excluding glands), shorter, more elliptic cells of their disc corolla throats, shorter disc style branches and collecting appendages, and a tendency for reduction of the pappus. The pappus is formed of capillary bristles in *Gundlachia*, *Bigelowia*, *Euthamia*, and *Xylothamia*, but in the other genera, which have a reduced chromosome number, the pappus is highly modified or reduced to a crown or series of short scales. In this group of specialized taxa, the disc corolla lobes are also more shallowly cut than in the other genera. Most plants of the *Gutierrezia* lineage have trinerved, punctate glandular, and commonly glutinous, leaves, as do some taxa within the *Solidago* lineage. The capitulescence in the *Gutierrezia* lineage is characteristically flat topped, strongly so in most of the taxa, often with the heads in small glomerules; this is also true within *Solidago* and some genera of the *Petradoria* group. Within the Solidagininae, the heads of relatively dense, flat topped capitulescences tend to open simultaneously and cannot technically be referred to as either cymoid or corymboid. In fewer flowered capitulescences, such as in some genera of the *Petradoria* group, the heads are clearly in a cymoid arrangement. Nevertheless, it seems likely that all flat topped capitulescences in the subtribe are homologous. In general, the *Gutierrezia* group is more homogeneous than the *Petradoria* group in capitulescence, head size, leaf morphology, and ray and disc corolla morphology; some taxa of both groups have highly modified pappus, and within both groups variation exists in almost all features.

The relationship of *Brachychaeta* and *Brintonia* to *Solidago*

A position of anther filament insertion similar to that in the *Gutierrezia* lineage occurs in two species sometimes treated within *Solidago*, but each has also been segregated as a monotypic genus: *Brachychaeta* Torr. & Gray (*Brachychaeta sphacelata* [Raf.] Britton = *S. sphacelata* Raf.) and *Brintonia* E. Greene (*Brintonia discoidea* [Ell.] E. Greene = *S. discoidea* Ell.). Both were treated at the generic rank by Kapoor & Beaudry (1966), although they described the filaments of *Brintonia* as inserted below the tube apex.

Solidago sphacelata (*Brachychaeta*) occurs in Kentucky, Virginia, North Carolina, Tennessee, Georgia, and Mississippi. It has been treated as *Solidago* by all recent accounts of the North American flora and by regional floras (e.g.,

Radford, Ahles, & Bell 1968; Cronquist 1980). Even its original authors, Torrey & Gray, observed differences from *Solidago* only in its cordate leaves and very short pappus, which comprises a whorl of bristles 0.5-1.0 mm long but otherwise similar to bristles of typical *Solidago* taxa.

Solidago discoidea (*Brintonia*) occurs across the Gulf coastal plain from Florida to Louisiana. Radford, Ahles, & Bell (1968) treated it as a species of *Solidago*. Cronquist (1980), however, separated it as a monotypic genus, but he provided no rationale for treating it at this rank, nor for consistency did he explain why he maintained *Brachychaeta* within *Solidago*. The heads of *S. discoidea* are eradiate, and the disc corollas are white, commonly with a purple tinge; its other features are typical of *Solidago*, although it produces pappus bristles with dilated apices, which are not common in other species.

On the basis of leaf anatomy, Anderson & Creech (1975) found both *Brachychaeta* and *Brintonia* more similar to "typical" *Solidago* than to any proposed generic segregates of *Solidago*, although *Euthamia* was the only such of the *Gutierrezia* lineage included in their sample. *Brachychaeta* and *Brintonia* also are similar to *Solidago* in their woodland habitat, rhizomatous habit, cauline leaves gradually reduced upwards, relatively thin, eglandular, and net veined leaves with sharply serrate margins, and sparsely pilose vestiture. The heads of *Brachychaeta* are secund on curving branches, while those of *Brintonia* are arranged in a thyrsoid capitulescence; both of these capitular arrangements are common in *Solidago*.

The closest relatives of *Solidago sphacelata* are almost certainly the species of "typical" *Solidago*, *S. brachyphylla* Chapm. and *S. auriculata* Shuttl. ex S.F. Blake. Both of these species have secund flowering branches, cordate lower leaves with margined petioles, and definitely shortened pappus bristles (ca. 2 mm long, half the length of the disc corollas). And significantly, the anther filaments are inserted at the tube-limb junction exactly as in *S. sphacelata*. Fernald (1950) hypothesized that *S. sphacelata* hybridizes with *S. ulmifolia* Muhl. ex Willd., but the latter, while perhaps also closely related, has anther filaments inserted below the tube apex. The two closest relatives of *S. sphacelata*, as hypothesized here, are allopatric with it and apparently do not form natural hybrids.

Solidago discoidea is almost certainly the sister species of the only other white flowered species clearly within *Solidago*, *S. bicolor* L. The latter has a thyrsoid capitulescence, white ray corollas, anther filaments inserted at the tube-limb junction, and pappus bristles with dilated apices. *Solidago discoidea* is set apart in taxonomic rank from this species solely on the basis of its discoid heads, and at least one other species of *Solidago* (*S. brachyphylla*) is eradiate. Many genera of Astereae comprise both radiate and eradiate taxa. *Solidago discoidea* and *S. bicolor* in turn appear to be closely related to the typically yellow rayed *S. macrophylla* Pursh, to which they are otherwise similar in capitulescence, corolla morphology, and pappus. *Solidago caesia* L. also is

similar in capitulescence and disc corolla morphology and probably closely related to these.

The two species groups discussed above (those centered around *Solidago sphacelata* and *S. discoidea*) have similar disc corollas, and they are similar in this respect to at least one other group among the *Solidago* species included in the present survey, the *S. wrightii* A. Gray-*S. petiolaris* Ait. species complex (Nesom 1990), which produce thyrsoid to flat topped capitulescences. This feature of corolla morphology (tube-limb filament insertion), which is invariable within the *Gutierrezia* lineage, also appears to be a reliable marker of species groups within *Solidago*, and in a broader survey of species within the genus, it may prove to be critical in identifying major lineages. In fact, the species of my sample with this feature correspond exactly to one of the two major species groups within *Solidago* identified by Anderson & Creech (1975), those lacking secretory cavities and mostly with bifacial mesophyll.

The status of *Oreochrysum*, *Oligoneuron*, and *Unamia*

Two other yellow flowered generic segregates of *Solidago* have been proposed: *Oreochrysum* Rydb. (monotypic) and *Oligoneuron* Small (ca. 6-8 species). Both of these have a typical *Solidago*-like habit and produce flat topped capitulescences. Because most of the genera related to *Solidago* (those of the *Gutierrezia* and *Petradoria* groups), and yet other infrageneric groups within *Solidago* (e.g., the *S. petiolaris* group), produce similar capitulescences, it can be assumed that this is the primitive form within *Solidago*. The anther filaments of both *Oreochrysum* and *Oligoneuron* are inserted at midtube, and the morphological justification for segregating them taxonomically relies primarily on characters of the phyllaries. Rydberg emphasized the distinctiveness of the long style appendages of *Oreochrysum*, but other species within *Solidago* have similar ones (e.g., *S. macrophylla* Pursh and even the generitype, *S. virgaurea* L.). The phyllaries of *Oligoneuron* are multinerved, but so are they in other species (e.g., *S. hintoniorum* Nesom). Both taxa may be kept within *Solidago* on the basis of morphology, in agreement with Anderson & Creech (1975). The molecular data of Morgan (1990), however, whose sample of the subtribe included three genera, showed *Oreochrysum* more closely related to *Tonestus* than to *Solidago*. The relationship of a third generic segregate, the white flowered *Unamia* E. Greene (*Solidago ptarmicoides* [Nees] Boivin), to *Solidago* is more complex and is considered within part of a separate paper (Nesom in prep.).

The relationship of the *Gutierrezia* and *Solidago* lineages

The discoid heads, shortened pappus, and distinctive filament insertion found in *Solidago sphacelata* and *S. discoidea*, as well as those species putatively related to them, are features otherwise uncommon in *Solidago* but characteristic of the *Gutierrezia* lineage. The style branches and collecting appendages within the genus *Solidago* are mostly short lanceolate to deltate, similar to those found in the taxa of the *Gutierrezia* lineage, while in the remaining genera of the *Petradoria* group, the style branches and appendages are mostly linear. Further, *Thurovia* and occasional individuals of *Gutierrezia texana* (DC.) Torr. & Gray produce secund flowering branches, with the heads all positioned on one side, a feature characteristic of many *Solidago* species. Conversely, several groups of *Solidago* produce distinctly flat topped capitulescences, which are characteristic of most of the other genera of Solidagininae, in both the *Gutierrezia* and *Solidago* lineages. While the vestiture of *Solidago* is in general different from that of its close relatives, at least two species, *S. odora* Ait. and *S. chapmanii* A. Gray, have punctate glandular leaves, although the anatomy of the glands is different from those of the remainder of the Solidagininae (Anderson & Creech 1975). In summary, variability within *Solidago* includes most of the features that characterize the *Gutierrezia* lineage, perhaps providing an indication of the ancestral position of the former with regard to the latter (Fig. 1).

The molecular data of Suh and Morgan, while highly incomplete with respect to the taxa of Solidagininae, contradict an hypothesis that places *Solidago* as potentially ancestral to both the *Gutierrezia* lineage and the remainder of the *Solidago* lineage (the *Petradoria* group) (Fig. 1). The two species of *Solidago* in Suh's analysis (*S. altissima* L. and *S. nemoralis* Ait.), both with a similar capitulescence and midtube filament insertion, form the sister group of the *Petradoria* group, and these two clades in turn are phylogenetically co-ordinate with the *Gutierrezia* lineage. In future molecular studies, it will be critical to investigate a wider range of species within *Solidago*, since I have found no morphological specialization that could be used to support a closer relationship between *Solidago* and the *Petradoria* group than between *Solidago* and the *Gutierrezia* group.

Solidago is by far the largest genus among its relatives and also the most widespread, with species covering all of North America. It becomes much less common southward and is represented in South America by only a single species, which nevertheless appears to be autochthonous there. *Solidago* sensu stricto also occurs in Europe and Asia, where it is represented perhaps by only one variable species (the generic type) or a small group of closely related ones. The other genera of the *Solidago* lineage (the *Petradoria* group) are primarily confined to western North America. Those of the *Gutierrezia* lineage extend from the Caribbean Islands and eastern North America, to western North

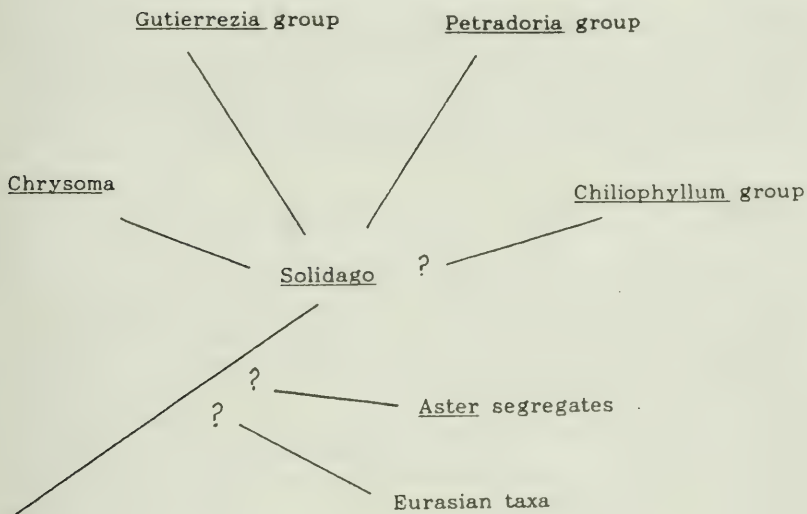


Figure 1. Phylogenetic hypothesis for the subtribe Solidagininae.

America and México. *Xylothamia* and *Gymnosperma* have primarily Mexican distributions. *Gutierrezia* occurs in México and the western United States and has a disjunct group of highly polyploid species in South America (Solbrig 1966).

Solidagininae in South America

A group of closely inter-related genera endemic to South America appears to belong to the Solidagininae: *Chiliophyllum* Phil., *Chiliotrichium* Cass., *Chiliotrichopsis* Cabrera, *Nardophyllum* Hook. & Arn., *Parastrephia* Nutt., and probably *Aylacophora* Cabrera. Several of these genera were included by Hoffmann (1890) in his conspectus of the subtribe. They are all small shrubs with numerous, relatively small heads, yellow flowers, reduced rays, disc corollas with spreading-reflexed or coiling lobes and anther filaments inserted at the tube-limb junction, linear, somewhat "Solidagolike" style appendages, and in some the vascular traces of the style appendages are prominently broadened. The leaves are ericoid, densely tomentose beneath. Punctate glands are produced in a few of the species, but most have numerous, small, epiphyllous glands. There is a strong tendency in several of the genera for the receptacles to produce long pales, and the achenes are often densely glandular. The chromosome number has not been reported for any of the taxa. Apart from

Gutierrezia, these are the only South American taxa that appear to belong to the subtribe, based on their morphology, but the nature of their relationship to the rest of the subtribe is not clear (Fig. 1). The present study is incomplete insofar as it has not taken extra-American taxa into account, but these will be covered as my sample of genera of *Astereae* expands.

The position of *Chrysoma*

Chrysoma, a monotypic genus of the southeastern United States, is a woody shrub that produces small heads in "corymbs," yellow rays reduced in size and number, sometimes completely absent, and deeply cut, spreading-recurved disc corolla lobes. These features and its style appendage morphology place it in the *Solidagininae*, where, however, it is not obviously allied to any of the genera. Greene (1895) enlarged *Chrysoma* to include *Gundlachia*, which is similar in habit and leaf shape, and the geographic position of *Chrysoma* suggests that it would be a member of the *Gutierrezia* lineage. In contrast, the near perfect correlation between the distinctive molecular characteristics and the morphology (particularly the filament insertion and punctate glandular vestiture) of the previously identified members of the *Gutierrezia* lineage suggests that *Chrysoma* is not a part of that group. The anther filaments in *Chrysoma* appear to be inserted at midtube, although the disc corollas are greatly elongated, making the tube-limb transition difficult to identify. The leaf surface is composed of subisodiametric areoles, giving a snake-skin appearance, each areole surrounded by a sunken reticulum that appears to be the source of a resinous exudate. Further, the phyllaries of *Chrysoma* have an orange resinous midvein continuous from base to tip, more similar to those of *Solidago* than to the gland tipped phyllaries of the *Gutierrezia* lineage, and the leaves of *Chrysoma* do not produce storage parenchyma like that found in *Euthamia* and *Gundlachia* (Anderson & Creech 1975). A more precise phylogenetic positioning of this anomalous species awaits further data, but it may have been derived from the ancestral *Solidago*-like complex independently of both the *Gutierrezia* lineage and the genera of the *Petradoria* group (Fig. 1).

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CORRECTION IN NOMENCLATURE FOR *TOMENTAURUM*
(ASTERACEAE: ASTEREEAE)

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ABSTRACT

An earlier name has been discovered for the plant designated by the combination *Tomentaurum vandeenderorum* (B. Turner) Nesom.

KEY WORDS: *Tomentaurum*, Asteraceae, Astereae, nomenclature

To describe the single species in the genus *Tomentaurum* Nesom from Chihuahua, México (Nesom 1991), I used the epithet supplied to it as *Heterotheca vandeenderorum* B. Turner. I have since discovered that the species was earlier named by Sereno Watson as *Aplopappus* and subsequently transferred to *Chrysopsis* by E.L. Greene. The correct name in *Tomentaurum* must be as follows:

Tomentaurum niveum (S. Watson) Nesom, *comb. nov.* BASIONYM: *Aplopappus niveus* S. Watson, Proc. Amer. Acad. Arts 23:277. 1888. TYPE: MÉXICO. Chihuahua: gravelly border of streams in the Sierra Madre, Sep 1887, C.G. Pringle 1300 (HOLOTYPE: GH). *Chrysopsis nivea* (S. Watson) E. Greene, Pittonia 3:43. 1896.

Additional specimen examined: MÉXICO. Chihuahua. Mpio. Bocoyna, along old railroad bed and old road between Creel and Bocoyna near tunnel, 13 Jul 1973, Bye 4209 (CM).

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Nesom, G.L. 1991. *Tomentaurum* (Asteraceae: Astereae), a new genus of goldenaster from Chihuahua, México. *Phytologia* 71(2):128-131.

HETEROTHECA CHIHUAHUANA (COMPOSITAE: ASTEREEAE), NEW
SITES AND OBSERVATIONS ON ITS TYPE LOCALITY

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ABSTRACT

Heterotheca chihuahuana has previously been reported only from the state of Chihuahua, México, but recent collections extend its range into west central and southern Durango. Its type locality is almost certainly from southernmost Chihuahua.

KEY WORDS: *Heterotheca*, Asteraceae, Astereae, México

In the original description of *Osbertia chihuahuana* Turner & Sundberg, its authors (1986) noted that it was known from only a single collection, and they mapped the type locality in west central Chihuahua (México: Chihuahua. Llano Grande, 10 May 1960, *Pennington 59* (HOLOTYPE: TEX). Based on its similarities to *Heterotheca mexicana* Harms ex B. Turner and *H. vanderendorum* B. Turner, Turner (1987) transferred the species to the genus *Heterotheca*.

At the present time, CIIDIR-IPN-Unidad Durango is developing a Flora of Durango. In the course of a collecting program towards this end, recent collections of *Heterotheca chihuahuana* show that the species has a much wider distribution than originally known. These new collections, which are from the Sierra Madre Occidental of Durango, are mapped in Figure 1 and reported in detail here: MÉXICO. Durango: 7.5 km al SE de La Guacamayita (Sierra Azul) Mpio. de El Mezquital, alt. 2840 m, bosque de *Quercus sideroxyla*, *Quercus* sp., *Cupressus*, *Pinus* sp., 23-V-87, M. González y S. Acevedo 2232 (CIIDIR); 7.5 km al NE de Llano Grande de Milpillas Chico, Mpio. de Pueblo Nuevo, alt. 2300-2350, bosque de *Quercus*, *Pinus*, *Cupressus*, y *Alnus*, 25-V-87, M. González y S. Acevedo 2287 (CIIDIR); San Miguel de Cruces, Mesa del Roble, Mpio. de San Dimas, alt. 2740 m, bosque de *Pinus durangensis*, *P. teocote* con *Juniperus*, *Arbutus*, *Arctostaphylos*, 26-V-90, A. García y S. Acevedo 349 (CIIDIR); San Miguel de Cruces, 250 m, al oeste de Veredas

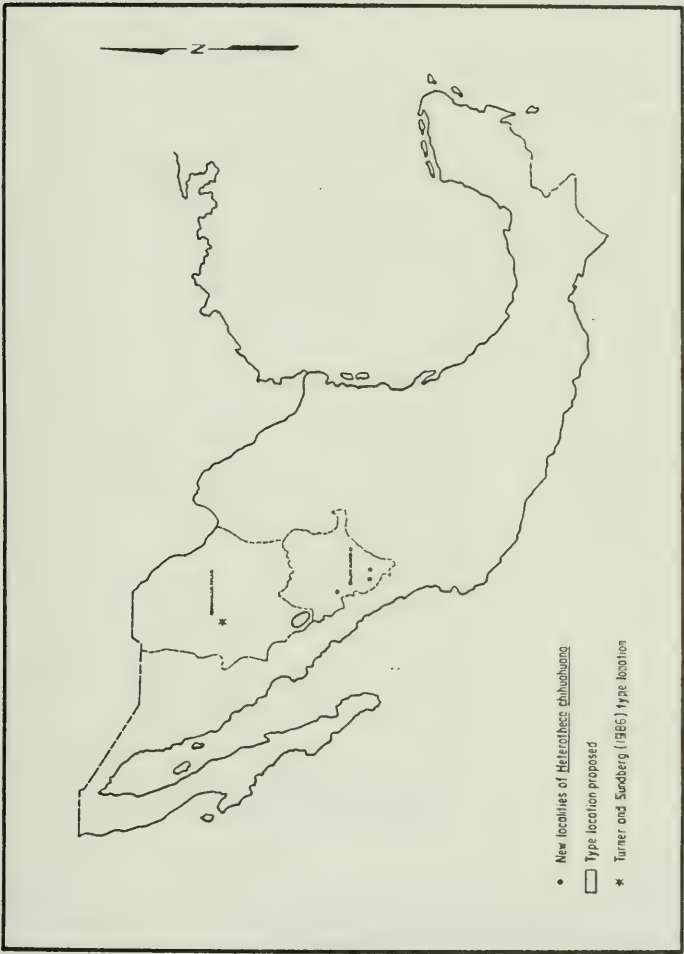


Figure 1. Updated distribution map of *Heterotheca chihuahuana*.

camino a Puertecillas, Mpio. de San Dimas, alt. 2760 m, bosque de *Pinus teocote*, *P. ayacauite* con *Juniperus*, 27-V-90, A. García, M. González, y S. Acevedo 384 (CIIDIR).

The new collections and a reconsideration of the type locality of *Heterotheca chihuahuana* lead me to believe that the original collection was made in southern Chihuahua rather than the west central part of the state, as mapped by Turner & Sundberg (1986). The label of the type specimen noted that the plants were used as pasturage for domestic animals by the Tepehuan Indians and that its collection locality was "Llano Grande." Its collector, Campbell Pennington, made a number of plant collections in the area inhabited the Tepehuans and published a book about the Northern Tepehuans from both historical and anthropological points of view (Pennington 1969). There are many places called Llano Grande along the Sierra Madre Occidental, since this name means literally "big plain," a landscape frequently encountered in the area. The Llano Grande noted on the collection label, however, almost certainly refers to a locality in Chihuahua where the Tepehuans were settled long before 1960. In fact, Pennington (1969) observed that the native people live in the municipios of Morelos and Guadalupe y Calvo, Chihuahua, which are in the southernmost part of the state near the border of Durango. Figure 1 shows the probable area of the type collection, which is biogeographically more closely related to the recent collections to the south.

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BOOKS RECEIVED

After the Ice Age, The Return of Life to Glaciated North America. E.C. Pielou. The University of Chicago Press, Chicago, Illinois 60637. 1991. 366 pp. ix. \$24.95 (hardcover with dust jacket). ISBN 0-226-66811-8.

Pielou's book describes the most recent continental glaciation in North America and the effects of that glaciation on the organisms found in North America today. Topics treated in the book range from evidence for the presence or absence of glaciers in any given area, to explanations (based on glaciation patterns) of present distributions of certain organisms. The concept of geological dating is described, as is interpretation of fossil evidence to determine past vegetation in a region, and migration of vegetation through time. After a section describing plant and animal life at the glacial maximum, the following section describes the biotic changes in response to the physical changes caused by melting of the glaciers. Information contained in these sections is used as a foundation to place more recent events (major extinctions, etc.) and present day distributions in context. The text is extensively referenced to the ecological literature on the subject, is illustrated with line drawings, and is written in a style easily interpreted by the nonscientist as well as the scientist.

Anales del Instituto de Biología, Serie Botanica, vol. 60(1). Fernando Chiang C. (ed.). Universidad Nacional Autónoma de México, D.F. México. 1990. 103 pp. Price unknown. ISSN 0374-5511.

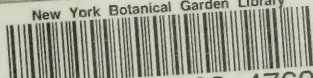
This volume is dedicated to Dr. Teófilo Herrera Suárez in celebration of his 45 years as a scientific investigator. Ten papers are included, most written in Spanish, two in English, and one in French. All papers are accompanied by Spanish by Spanish abstracts, and all except the paper in French have English abstracts. Topics of the papers range from studies of yeast in fermentation of certain foodstuffs, to descriptions of new taxa in Acanthaceae, Euphorbiaceae, and Thymelaeaceae, to medicinal plants of Ocotlán, Oaxaca.

British Plant Communities, Woodlands and Scrub, vol. 1. J.S. Rodwell (ed.). Cambridge University Press, 40 West 20th Street, New York, New York 10011. 1991. 395 pp. x. \$150.00 (hardcover). ISBN 0-521-23558-8.

This is the first of an anticipated five volumes describing the vegetation of Britain (including the associated islands of Great Britain, but not Ireland. Vegetation sampling was completed using a 10 X 10 km grid pattern as a foundation. During the sampling phase of the project, data (description of the site, cover class for each species observed, geology, soil profile, etc.) from nearly 35,000 sites were collected. Sampling at each site involved delimitation of plots (of various sizes and shapes, depending on the specific site to be sampled). Overall, sampling sites were distributed through 80% of the 10 X 10 km grids, with only major metropolitan areas and eastern Scotland showing significant gaps in the sampling pattern.

Each type of woodland or scrub community is described, and its distribution plotted by dots located the grids were that vegetation type was sampled. Discussions of each vegetation type include synonyms used in previous works to refer to the same vegetation type, a list of species consistently found in that vegetation type, a list of rare species in that vegetation type, and a summary of the environmental factors that cause that vegetation type to be found in certain areas. Subcommunities are listed and described, and their geographic distributions are noted. All in all, this is an exhaustive summary of vegetation patterns in Britain and will be very useful to anyone undertaking ecological studies in that area.

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Authors should arrange for two workers in the appropriate field to review the manuscript before submission. Copies of reviews should be forwarded to the editor with the manuscript. Manuscripts will not be published without review.

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